February 1987 Volume 61, Number 1

NORTHWEST SCIENCE

CONTENTS

1 Seed Dispersal of Engelmann Spruce in the Intermountain West—**Ward W. McCaughey and Wyman C. Schmidt**

7 Branching and Terminal Growth of Western Redcedar—**Tracey Parker and Frederic D. Johnson**

13 Tentative Growth Curve for *Rhizocarpon geographicum s. l.* in Stroud Basin, Wind River Range, Western Wyoming—**William C. Mahaney**

20 Survival of *Veratrum viride,* a Robust Herbaceous Plant, when Buried by Volcanic Tephra—**Donald B. Zobel and Joseph A. Antos**

23 Survey of Mammal Damage to Tree Fruit Orchards in the Okanagan Valley of British Columbia—**Thomas P. Sullivan, John A. Krebs, and H. Anthony Kluge**

32 Comparison of Age Determinations Based on Scales, Otoliths and Fin Rays for Cutthroat Trout from Yellowstone Lake—**Wayne A. Hubert, George T. Baxter, and Mark Harrington**

37 Effect of Alternative Tillage Systems on Rodent Density in the Palouse Region—**Donald R. Johnson**

41 Factors Influencing the Distribution of *Wolffia columbiana* and *Wolffia punctata* (Lemnaceae)—**Leslie Kline and Bruce McCune**

44 Population Monitoring of *Phacelia verna:* A Federal Candidate Species—**Russell N. Holmes**

50 Northern Idaho Citizens Survey on Nongame Wildlife and Idaho Income Tax Checkoff Program—**Ronald B. Newton, Kerry P. Reese and Wayne E. Melquist**

55 Estimating Herbaceous Yield from Species Frequency—**Jeffrey C. Mosley, David B. Wester, and Stephen C. Bunting**

60 Survival of Douglas-fir Injected with the Fumigants Chloropicrin, Methylisothiocyanate or Vorlex—**W. G. Thies and E. E. Nelson**

Northwest Scientific Association

(Founded 1923)

The Northwest Scientific Association, an affiliate of the American Association for the Advancement of Science, is an association representative of the basic and applied sciences and of social sciences.

Membership in the Northwest Scientific Association, which includes a subscription to *Northwest Science,* is open to individuals for $14 per year ($8 per year for students). Institutional memberships: (Washington, Idaho, Oregon, Western Montana, and British Columbia) less than 3000 students, $30; 3000 students or more $40. All other subscribers, $25 per year. Sustaining membership, $25 per year for individuals and $100 per year for organizations, institutions, or agencies. Subscriptions are for the calendar year only.

Send change of address, payment of dues, or requests for undelivered issues to the Treasurer.

Editor of *Northwest Science*

Kenneth V. Kardong
Department of Zoology
Washington State University
Pullman, Washington 99164-4220

Officers of the Association

President Donald Hanley*
Washington State University
c/o University of Washington
Seattle, Washington (1987)

President-Elect Steven D. Tesch
Oregon State University
Corvallis, Oregon (1989)

Secretary Robert L. Carr
Eastern Washington University
Cheney, Washington (1987)

Treasurer Robert K. Moseley
The Nature Conservancy
1221 South Main Street
Moscow, Idaho 83843 (1989)

Past President Ray A. Soltero
Eastern Washington University
Cheney, Washington (1986)

Trustees:

Robert Antibus
University of Montana
Missoula, Montana (1988)

Wilbert R. Danner
University of British Columbia
Vancouver, B.C. (1989)

Lee E. Eddleman
Oregon State University
Corvallis, Oregon (1987)

William H. Emmingham
Oregon State University
Corvallis, Oregon (1987)

Kenneth Hammond
Central Washington University
Ellensburg, Washington (1989)

Hubertus Kohn
Western Washington University
Bellingham, Washington (1987)

Larry Larson
Oregon State University
Corvallis, Oregon (1988)

Gilbert B. Pauley
University of Washington
Seattle, Washington (1989)

M. A. Radwan
U.S. Forest Service
Olympia, Washington (1987)

William R. Rayburn
Washington State University
Pullman, Washington (1989)

W. H. Rickard
Pacific Northwest Laboratory
Richland, Washington (1988)

Harry Smith
University of British Columbia
Vancouver, B.C. (1988)

George G. Spomer
University of Idaho
Moscow, Idaho (1987)

Steven D. Tesch
Oregon State University
Corvallis, Oregon (1988)

David H. Wagner
University of Oregon
Eugene, Oregon (1989)

*Term of office expires in the year given in parentheses.

February 1987 Volume 61, Number 1

NORTHWEST SCIENCE

Editor	Kenneth V. Kardong	Washington State University
Managing Editor	Fred Bohm	Washington State University
Associate Editors		
Aquatic Biology	Gary L. Larson	U.S. National Park Service/ Oregon State University
Botany	Suzanne M. Schwab	Eastern Washington University
Chemistry and Physics	Frank L. Curzon	University of British Columbia
Engineering and Mathematics	Gary L. Sheldon	Washington State University
Forestry	James K. Agee	U.S. National Park Service/ University of Washington
Geology	Franklin F. Foit, Jr.	Washington State University
Social Sciences	Philip D. Young	University of Oregon
Soils	Robert L. Edmonds	University of Washington
Wildlife Biology	Margaret A. O'Connell	Washington State University
Zoology	Kerry Paul Reese	University of Idaho

CONTENTS

1 Seed Dispersal of Engelmann Spruce in the Intermountain West—**Ward W. McCaughey and Wyman C. Schmidt**

7 Branching and Terminal Growth of Western Redcedar—**Tracey Parker and Frederic D. Johnson**

13 Tentative Growth Curve for *Rhizocarpon geographicum s. l.* in Stroud Basin, Wind River Range, Western Wyoming—**William C. Mahaney**

20 Survival of *Veratrum viride,* a Robust Herbaceous Plant, when Buried by Volcanic Tephra—**Donald B. Zobel and Joseph A. Antos**

23 Survey of Mammal Damage to Tree Fruit Orchards in the Okanagan Valley of British Columbia—**Thomas P. Sullivan, John A. Krebs, and H. Anthony Kluge**

32 Comparison of Age Determinations Based on Scales, Otoliths and Fin Rays for Cutthroat Trout from Yellowstone Lake—**Wayne A. Hubert, George T. Baxter, and Mark Harrington**

37 Effect of Alternative Tillage Systems on Rodent Density in the Palouse Region—**Donald R. Johnson**

41 Factors Influencing the Distribution of *Wolffia columbiana* and *Wolffia punctata* (Lemnaceae)—**Leslie Kline and Bruce McCune**

44 Population Monitoring of *Phacelia verna:* A Federal Candidate Species—**Russell N. Holmes**

50 Northern Idaho Citizens Survey on Nongame Wildlife and Idaho Income Tax Checkoff Program—**Ronald B. Newton, Kerry P. Reese, and Wayne E. Melquist**

55 Estimating Herbaceous Yield from Species Frequency—**Jeffrey C. Mosley, David B. Wester, and Stephen C. Bunting**

60 Survival of Douglas-fir Injected with the Fumigants Chloropicrin, Methylisothiocyanate or Vorlex—**W. G. Thies and E. E. Nelson**

Announcements

FROM NWSA PRESIDENT, Donald P. Hanley

Annual Meeting 1987

Meeting Registration Information and the Call for Papers have been mailed for the annual meeting to be held March 26-28, 1987 at Pacific Lutheran University in Tacoma, WA. Please pass the information along to a colleague if you are unable to attend. Dr. David H. Hansen, the general program chairman, has assembled an excellent meeting. In addition to the contributed papers, three exceptional symposia are planned: Puget Sound: Biological Health and Population; Ecology and Physiology of Upper Slope Conifers; and Current Field Research in Northwest Archaeology. Please plan to attend!

Annual Meeting 1988

Plans are developing for the 1988 NWSA Annual Meeting to be held in March 1988 at Southern Oregon State College. Dr. Claude W. Curran, Director, School of Social Science, has agreed to be the general program chairman.

NWSA Membership Drive

The NWSA Governing Board is initiating a membership drive to recruit additional scientists and students into our Association. A new promotional folder is being developed as well as faculty mailing lists for member universities. Membership drive details will be explained at the annual business meeting in March. With your help we will be able to introduce to other scientists the benefits of NWSA membership.

Awards and Honors

The deadline for mailing nominations for Outstanding Northwest Scientist and for Honorary Life Member has been extended. Please submit nominations, a letter with background information on the candidate is appropriate, *as soon as possible* to Dr. Larry Larson, Rt. 3 Box 3429, La Grande, OR 97850

Research Grants

The deadline for mailing applications for Research Grants has been extended. Please submit applications *as soon as possible* to Dr. George Spomer, Department of Biological Sciences, University of Idaho, Moscow, ID 83843.

Welcome New Associate Editors

We have four new associate editors: Dr. Suzanne M. Schwab, Eastern Washington State University, in Botany; Dr. Gary L. Larson, National Park Service/Oregon State University, in Aquatic Biology; Dr. Margaret A. O'Connell, Washington State University, in Wildlife Biology, and Dr. Kerry Paul Reese, University of Idaho, in Zoology. Thank you for joining the team of dedicated associate editors of *Northwest Science.*

In Memorium

Friends will be saddened by the death of Willis B. Merriam in October 1986. From 1937 to 1941, and again from 1956 to 1960 he was Secretary/Treasurer of the Northwest Scientific Association and an honorary life member. In addition to his other work for our Association, he prepared a history from its founding up until 1960.

Ward W. McCaughey and **Wyman C. Schmidt**
Intermountain Research Station, USDA Forest Service
Forestry Sciences Laboratory, Montana State University, Bozeman, Montana 59717

Seed Dispersal of Engelmann Spruce in the Intermountain West

Abstract

The amount and distance Engelmann spruce seed dispersed into openings was found strongly related to total seed production and quantity of spruce basal area in the adjacent windward stand. This study, conducted at 10 locations in the Intermountain West, showed that spruce seeds were dispersed as far as 201 m from the windward edges of openings, but the amount of seed decreased rapidly from 0 to 120 m. At 120 to 201 m from seed source, the number of dispersed seeds stabilized at a low level. Nearly 95 percent of all spruce seeds dispersing into openings fell within 120 m of the windward seed source. Two models were developed to illustrate these dispersal characteristics. Seed dispersal information is an important factor in making knowledgeable decisions concerning natural and artificial regeneration in the spruce forest type.

Introduction

Insufficient stocking of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) natural regeneration on cutover areas has been a persistent problem in the Intermountain area since the 1950's. Cone production varies by year, and even in the best cone producing years, seed production can be reduced by cone and seed insects, rodents, birds, and other natural factors such as frost (Roe and Schmidt 1964, Schmidt *et al.* 1976, Shearer 1959). Even large numbers of first-year germinants resulting from heavy seed crops do not guarantee sufficient spruce establishment. Most established seedlings are usually found near timber edges rather than farther into openings (Noble and Ronco 1978).

Seed-dispersal information provides us with knowledge of how much and how far spruce seed disseminates from a source. Reliable dispersal information and a knowledge of seed:seedling ratios on varying site conditions help silviculturists make sound biological decisions concerning size and shape of cutting areas. Seedling ratios vary considerably in relation to seedbed condition and environmental and biotic factors (Alexander 1983).

The amount and distance of Engelmann spruce seed dissemination was largely unknown in the Intermountain area when this study was initiated. First-year results from a bumper seed crop indicated that quantity of sound spruce seed dispersed into Intermountain clearcuts decreased rapidly as distance from the seed source increased, and then remained at low levels (Roe 1967). Because the data were from a single bumper seed crop, dispersal equations developed by Roe (1967) provide a much higher estimate of the quantity of spruce seed dispersed into clearcuts than yearly averages would indicate. Spruce produce good to bumper seed crops about once every 2 to 10 years depending on geographical location (Boe 1954, USDA in press).

The inverse relationship of seed dispersed in relation to distance from the seed source has been quantified for Engelmann spruce in the southern Rockies by Noble and Ronco (1978) and Alexander and Edminster (1983). White spruce (*Picea glauca* [Moench] Voss) and black spruce (*Picea mariana* [Mill.] B.S.P.) seed dispersal information is available for the northern Rockies in Canada by Dobbs (1976) and Payendeh and Haavisto (1982), respectively. This paper reports seed dispersal information for Engelmann spruce in the Intermountain area.

Methods

This study, designed to investigate seed dispersal characteristics of Engelmann spruce, was established on five National Forests in the Intermountain area—the Ashley, Dixie, and Uinta in Utah, the Teton (now Bridger-Teton) in Wyoming, and the Payette in Idaho. Ten study sites—one clearcut on each of two districts on each National Forest—were used to examine the seed dispersal.

Traps were used to collect spruce seeds dispersed in the uncut timber and into clearcuts. Seed traps were rectangular boxes approximately 0.61 m wide, 0.91 m long, and 10.2 cm deep. Each trap was covered on top by metal hardware cloth, which allowed spruce seed to fall into the traps, and by a tightly woven screen on the bottom, which held seeds in the trap but allowed air to flow through for drying seeds.

At each study site, two parallel rows of seed traps with 10 traps in each row were approximately 40 m apart at right angles to the windward timber edge (Fig. 1). The first seed trap in each row was 20 m inside the windward timber edge, and the second trap in each row was at timber edge. In each row, seed traps three to eight were placed at 20 m intervals into the clearcut from the timber edge, and traps 9 and 10 were placed at 40 m intervals beyond trap 8.

Dispersed seeds for the seed years of 1965 through 1968 were collected the spring following fall and winter seedfall. Collected seeds were cut and examined for soundness. Quantity of spruce seed on a per-hectare basis was calculated by multiplying the number of sound spruce seeds found in each trap by a per-hectare conversion factor. All further references to seed in this paper will be for sound spruce seed.

Stand basal area of Engelmann spruce was used as a measure of the seed production capability of the spruce seed source within the windward stand. Basal area values in square meters per hectare were determined for spruce trees 25.4 cm and larger in diameter at breast height (dbh). Spruce trees of this size were assumed to be sufficiently mature to produce seed. Basal area values for the 10 study locations ranged from 3.9 m^2 per ha up to 45.9 m^2 per ha (Table 1).

Data from all 10 study sites were combined to develop a seed dispersal model for Engelmann spruce, applicable to the Intermountain area. Seed dispersal data from individual study sites were pooled because of a large amount of yearly variation within and between study areas. We assumed that 1965 to 1968 represented an average four-year period because seed crops ranged from failure to bumper. Seed crop production was good in 1965, a failure in 1966, bumper in 1967, and fair in 1968. The four-year average number of spruce seeds found in each seed trap on a per-hectare basis was used as a measure of expected seed dispersal.

TABLE 1. Engelmann spruce basal area in the windward stand at each study area location.

National Forest	Location name	Basal area (m^2/ha)
Ashley	North Brownie Creek	3.9
Ashley	Paradise Peak	15.2
Dixie	Griffin Top	13.1
Dixie	Midway Summit	45.9
Payette	Corral Creek	26.6
Payette	Fisher Creek	8.3
Bridger-Teton	Mosquito Creek	6.2
Bridger-Teton	Togwotee	44.3
Uinta	Cold Springs	15.6
Uinta	Hidden Lake	20.7

Stepwise regression techniques were used to develop a seed dispersal model that best explained dispersal of spruce seeds into openings from the windward timber. Other dependent and independent variables tested during the development of a seed dispersal model include the following:

Dependent—The natural logarithm of the four-year average number of spruce seeds that dispersed into clearcuts at specific distances from the windward edge.

Independent—The number of spruce seeds that fell into seed traps 20 m inside the windward stand edge.

—The natural logarithm of the distance each seed trap was located from the windward stand edge.

The constant 40.2 m was added to all measurements in the analyses to avoid negative or zero distance values for traps at 1 chain into the timber and at timber's edge, respectively. The standard regression model used was:

$$Y = b_0 + b_1X_1 + b_2X_2 + \ldots + bnXn$$

Results and Discussion

Seed dispersal of Engelmann spruce into openings in this Intermountain area was positively correlated with spruce basal area and with the quantity of spruce seeds dispersed at the windward stand edge, and was negatively correlated with distance from seed source. These results

correspond with other findings from this Intermountain area (Roe 1967; Shearer 1985). A similar Colorado study also showed that numbers of sound spruce seeds falling at different distances into openings was highly correlated with distance from the source and the amount of seed falling under the uncut stand (Alexander and Edminster 1983). Measures of the spruce seed source were not used in the Colorado seed dispersal models, but estimates of seed production were examined on the basis of live crown and basal area of dominant and codominant spruce (Alexander *et al.* 1982).

In this study, the basal area of the spruce seed source was a strong determinant of the amount of seed dispersed (Fig. 2). For example, doubling the spruce basal area of the seed source from 15 to 30 m^2 quadruples the amount of seed dispersed at the timber edge. This relationship of basal area to seed dispersal held true at all distances up to 200 m from the windward seed source. However, in Colorado Noble and Ronco (1978) found no correlations between seed production and basal area, but they did find a positive relationship of seed production in the windward seed source with number of seeds dispersed at all distances from the source. They related differences in seed numbers at different distances to the quantity of seed produced in the adjacent stand, but not to the spruce basal area.

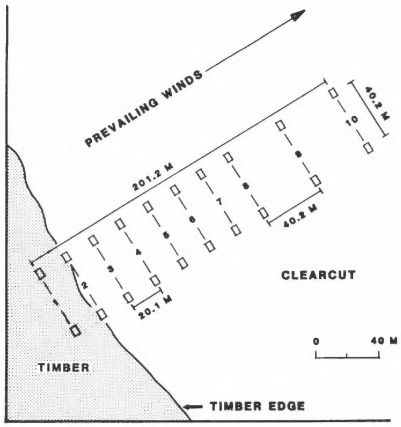

Figure 1. Seed trap locations in relation to windward stand edge—Engelmann spruce seed dispersal study.

Seed dispersal patterns show that as distance from the seed source increases, quantity of spruce seed decreases. In this study, Engelmann spruce seed was found to disperse up to 201 m from the windward edges of openings, but the quantity of sound seed decreased rapidly from 0 to 120 m from the windward stand edge and then remained at low levels or decreased slightly from 120 to 201 m. Almost 70 percent of all seed that dispersed into openings fell within 30 m and 95 percent fell within 120 m. This is similar to findings in the central Rocky Mountains where about 67 percent of the spruce seed dispersing into openings fell within 30 m of the windward stand edge and nearly 95 percent fell within 107 m (Alexander and Edminster 1983). This rapid decline in seedfall leveled off with only 1 percent of the spruce seeds falling under uncut stands dispersing as far as 183 m from the windward stand edge. In another Colorado study, about 50 percent of the seeds falling into clearcuts fell within 30 m of the windward edge (Noble and Ronco 1978). Numbers of seeds continued to decrease for a distance of 60 to 80 m from the windward stand edge, and then leveled off in the wider openings.

Two dispersal models were developed from these data to predict the number of spruce seeds that disperse into openings at varying distances from a windward seed source. The three-variable model requires a measure of spruce basal area and number of seeds dispersed at the windward edge, but the two-variable model only needs the basal area of the spruce seed source. Both models estimate the quantity of sound spruce seeds that can be expected at varying distances from a seed source. Yearly variation in seed-crop size is unaccounted for in the two-variable model. The quantity of spruce seeds dispersed is the expected yearly average over 4 years. The models and descriptions of the variables are shown for the three-variable and the two-variable models:

Three-variable model:

$$Y = [36.4481 + 0.0194\,(T * 1/D) + 350.5242\,(B * 1/D)]^2$$

$$R^2 = .84;\ MSE = 19312.56;\ n = 190$$

Two-variable model:

$$Y = [38.1525 + 792.3007\,(B * 1/D)]^2$$

$$R^2 = .69;\ MSE = 36317.32;\ n = 190$$

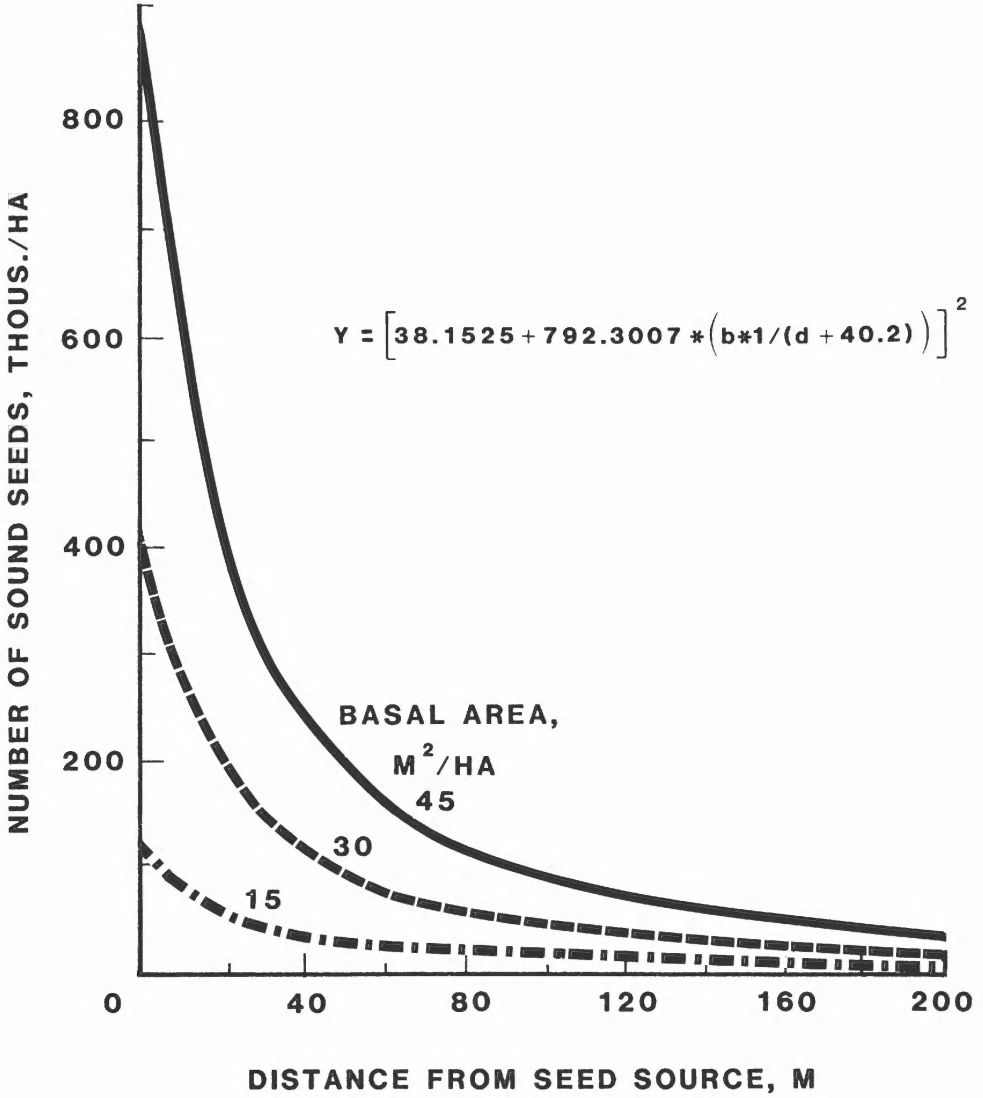

Figure 2. Seed dispersal patterns of Engelmann spruce at different distances from the seed source in relation to basal area of windward stand.

Variables:

Y = The 4-year average number of spruce seeds that disperse into clearcuts at specific distances from the windward stand edge.

B = The stand basal-area-per-hectare value of spruce trees in the windward timber that are 25.4 cm or larger at d.b.h.

T = The number of spruce seeds per hectare dispersed at the windward stand edge.

D = The distance each seed trap is located from the windward stand edge plus 40.23 m.

MSE = Regression mean square error.

n = Number of observations.

Table 2 was developed from the two-variable equation to show estimates of the number of spruce seeds dispersing into openings in relation to the basal area of spruce in the windward stand. The high mean square error indicates that a large amount of variability is not accounted for by the variables within the models.

The three-variable model provides a good prediction of seedfall into openings when spruce basal area of the windward stand and the amount of seed falling at timber edge are known. Its primary advantage over the two-variable model is that it adjusts for seedfall of a particular year. Simply measuring the basal area of spruce trees 25.4 cm and larger and reading seed traps at timber edge provide a good estimate of how much seed was dispersed at varying distances from timber edge. The primary disadvantage of the three-variable model is that it is a measure after seedfall.

The simpler two-variable model also has advantages and disadvantages. On the advantage side, it requires only a measurement of the basal area of spruce 25.4 cm and larger to provide an estimate of what might be expected in terms of amounts and distances of seed dispersal for an average year. As such, it provides an approximation before the fact, while the three-variable model depends on some measure of seed production for a given year. The primary disadvantage of the two-variable model is that it does not provide a good estimate for any given year, rather just an average. This is particularly important when predicting dispersal from a bumper seed crop.

There was no attempt in this study to measure seed dispersal from the leeward edge of cuttings nor to relate the quantity of sound spruce seeds to the number of resulting seedlings.

Knowledge of seed dispersal is an important factor in making defensible decisions concerning natural regeneration in the spruce forest type. Seed dispersal information coupled with knowledge of seed:seedling ratios for specific site conditions help managers in decisions on cutting shape and timing and method of site preparation. For example, Colorado studies (Alexander 1983) showed that, depending on site conditions, it may take from 32 to 417 spruce seeds to obtain one five-year-old spruce seedling. Seedling establishment of spruce is generally higher on scarified than on nonscarified sites (Alexander 1984, Fiedler and others 1985). Estimates of the quantity of seed dispersed at varying distances from the seed source and the seed:seedling ratios for various site preparation methods may suggest intensive scarification at the center of a clearcut and practically none near timber edge. It may also show that a large proportion of a proposed clearcut holds little prospect for successful natural regeneration, and that artificial regeneration will be needed if the manager proceeds with the cutting. As a result, both natural and artificial regeneration costs can be minimized by selecting proper silvicultural practices. Seed dispersal information helps make these silvicultural determinations.

Acknowledgments

We thank Arthur L. Roe, USDA Forest Service Research Silviculturist (retired) for designing this study and the Forest Service's Intermountain Region for establishing study plots and collecting the data.

TABLE 2. Predicted number of spruce seeds dispersed into openings at selected distances from the windward edge of stands of different basal area (estimates from two-variable model[1]).

Windward stand basal area (m^2/ha)	Distance from windward stand edge (meters) 0	40	80	80	120	160	200
				- - - - - - Thousands of seeds per hectare - - - - - - -			
5	19	8	5	4	3	3	
15	111	35	19	13	10	8	
25	281	81	41	26	19	15	
35	529	147	72	45	31	24	
45	855	233	112	68	47	35	

[1] $Y = [38.1525 + 792.3007 (B * 1/(D + 40.2))]^2$.

Literature Cited

Alexander, R. R. 1983. Seed:seedling ratios of Engelmann spruce after clearcutting in the Central Rocky Mountains. USDA For. Serv. Res. Note RM-246. Rocky Mtn. For. Range Exp. Sta., Fort Collins, Colo.

_____. 1984. Natural regeneration of Engelmann spruce after clearcutting in the central Rocky Mountains in relation to environmental factors. USDA For. Serv. Res. Note RM-254. Rocky Mtn. For. Range Exp. Sta., Fort Collins, Colo.

Alexander, R. R., and C. B. Edminster. 1983. Engelmann spruce seed dispersal in the Central Rocky Mountains. USDA For. Serv. Rocky Mtn. Res. Note RM-424. For. Range Exp. Sta., Fort Collins, Colo.

Alexander, R. R., R. K. Watkins, and W. C. Schmidt. 1982. Engelmann spruce seed production on the Fraser Experimental Forest, Colorado. USDA For. Serv. Res. Note RM-419. Rocky Mtn. For. Range Exp. Sta., Fort Collins, Colo.

Boe, Kenneth N. 1954. Periodicity of cone crops for five Montana conifers. Proc. Mont. Acad. Sci. 14:5-19.

Dobbs, R. C. 1976. White spruce seed dispersal in central British Columbia. For. Chron. 52:225-228.

Fiedler, C. E., W. W. McCaughey, and W. C. Schmidt. 1985. Natural regeneration in Intermountain spruce-fir forests—a gradual process. USDA For. Serv. Res. Pap. INT-343. Intermtn. For. Range Exp. Sta., Ogden, Utah.

Received 8 January 1986
Accepted for publication 27 March 1986

Noble, D. L., and Ronco, F. 1978. Seedfall and establishment of Engelmann spruce and subalpine fir in clearcut openings in Colorado. USDA For. Serv. Res. Pap. RM-200. Rocky Mtn. For. and Range Exp. Sta., Fort Collins, Colo.

Payendeh, B., and V. F. Haavisto. 1982. Prediction equations for black spruce seed production and dispersal in northern Ontario. For. Chron. 58:96-99.

Roe, A. L. 1967. Seed dispersal in a bumper spruce seed year. USDA. For. Serv. Res. Pap. INT-39. Intermtn. For. Range Exp. Sta., Ogden, Utah.

Roe, A. L., and W. C. Schmidt. 1964. Factors affecting natural regeneration of spruce in the Intermountain Region. USDA For. Serv. Intermtn. For. Range Exp. Sta., Ogden, Utah. Mimeo Rep.

Schmidt, W. C., R. C. Shearer, and A. L. Roe. 1976. Ecology and silviculture of western larch forests. USDA For. Serv. Tech. Bull. 1520.

Shearer, R. C. 1959. Western larch seed dispersal over clearcut blocks in northwestern Montana. Proc. Mont. Acad. Sci. 19:130-134.

_____. 1985. Establishment of conifers following broadcast burning on clearcuts in western Montana. University of Montana, Missoula. Dissertation.

U.S. Department of Agriculture, Forest Service. &In press.é Silvics of natural and naturalized trees of the United States and Puerto Rico. Agriculture Handbook. USDA, Forest Service. Washington, D.C.

Tracey Parker and **Frederic D. Johnson**
College of Forestry, Wildlife and Range Experiment Station
University of Idaho, Moscow, Idaho 83843

Branching and Terminal Growth of Western Redcedar

Abstract

Western redcedar (*Thuja plicata* Donn), family Cupressaceae, exhibits morphology quite distinct from its coniferous associates in the Pinaceae. Young Pinaceae trees can be reasonably aged, and past growth rates determined at a glance using major branch whorls. This is not true of western redcedar, or other members of the Cupressaceae. Growth morphology of western redcedar is described in terms of buds, leaves, and branching pattern as observed and measured in northern Idaho. A simple, nondestructive technique for aging western redcedar terminals for the previous three to six years is outlined. This technique for terminal location and aging appears adaptable to other members of the Cupressaceae.

Introduction

While investigating natural regeneration of western redcedar (*Thuja plicata* Donn) in northern Idaho (Parker 1979), we were faced with the problem of determining height, age and growth rate during each of the past several years. Western redcedar, in the family Cupressaceae, does not follow the familiar and regular growth pattern of its coniferous associates of northern Idaho (all members of the Pinaceae) in which a major whorl of branches on the main stem locates the beginning of each year's growth.

Thus, for two years, growth increments were observed on numerous western redcedar individuals. From these observations a method is described for finding the terminal, a feature deceptive in its location. Growth patterns are also described so observers can accurately measure annual height increments for the past several years.

Nondestructive aging of regeneration can provide quick and accurate height growth information; such knowledge is fundamental when evaluating the suitability of various sites and stand conditions for the growth of western redcedar.

Methods

Fifty-eight young cedars were dissected and comparisons made between growth rings and branching patterns. Measurements of leader growth on 35 young trees were made for one growing season on a variety of sites, including a middle-aged stand, road cuts and a clearcut. These observations coupled with the dissections resulted in methods for accurate location of terminals and determination of past years' height growth.

Morphology

To appreciate the complexity of western redcedar growth, a review of morphology is beneficial.

Buds

Western redcedar has buds without preformed shoots (Laubenfels 1953). Instead there are very small terminal resting buds which lack bud scales (Mitchell 1965, Aldhous & Low 1974), although buds are covered by numerous leaf primordia at various stages of development (Owens & Pharis 1971). Mitchell (1965) noted that *Thuja* shares this type of bud with *Chamaecyparis, Cupressus, Juniperus, Libocedrus* (all Cupressaceae), *Metasequoia* and Sequoia (both Taxodiaceae). Individuals of these genera are slow to start growth in the spring but grow steadily over a long growing season.

Kozolowski and Keller (1966) divided conifers of the temperate zone into two widely differing groups based on their shoot elongation. The first group, "predetermined," encompassing most of the Pinaceae, have buds which contain preformed shoots that are formed late in the growing season. After bud break in the spring, shoots elongate. It is possible for these trees to have a second flush of growth resulting in lamma shoots, typical in *Abies*. These "extra" shoots also rise from buds containing preformed shoots. After their extension another preformed shoot is produced to

overwinter as a bud. Kozolowski and Keller's (1966) second group, "non-predetermined," are certain members of the Cupressaceae, including *Thuja*, and Taxodiaceae; these have winter buds which do not contain fully preformed shoots. Both early and late leaves may be formed during the growing season of their expansion. No strong initial whorl of branches is produced, instead a series of more-or-less equal branches are produced throughout the growth period (Figure 1).

Predetermined trees (*Pinaceae*) complete shoot growth early in the growing season and there is a high correlation between shoot growth and previous year's weather. In contrast, non-predetermined trees (*Cupressaceae*) presumably use food reserves for initial elongation but use carbohydrates produced in the current season for further elongation. Williams (1968) found the height growth of western redcedar correlated well with current year's weather. A plausible explanation for this high correlation involves the lack of preformed shoots in western redcedar, and the use of current years' photosynthate for continual shoot elongation.

In our study, slow-growing, shade-suppressed trees often grew several centimeters early in the season and stopped. More vigorous open-grown trees grew early in the season, stopped in late summer during moisture stress, but resumed growth after fall rains had commenced, illustrating the environmentally responsive growth of western redcedar.

Mitchell (1965) found the pattern of growth and type of resting bud was closely correlated in conifers. He believes trees with very small buds and no predetermined shoot must make new tissue as conditions become favorable, hence the slow start in the spring. But, on the other hand, since they have little or no bud to prepare for winter they can continue growth as long as conditions permit, resulting in a long growing season. In this way western redcedar can respond if improved conditions occur late in the year.

We often found adventitious buds at the swollen branch junctions on main stems. From these buds may come more lateral branches or a new terminal if needed. In this study the terminals of three small western redcedar sample trees were browsed during the winter; all three had developed a new terminal by the following midsummer.

Leaves

Western redcedar usually has two wide, linear cotyledons which are flat in cross section (Figure 2-A). They are persistent but generally die after the first season. Juvenile leaves are subulate and flattened. These are mostly in whorls of four, although we found individuals with whorls of three (Figure 2-B&C). Juvenile leaves are slightly decurrent; the majority of the leaf extends at a right angle to the main axis. Vigorous seedlings may branch and produce mature foliage during the first year, but slow growing individuals may produce only juvenile leaves for several years (Figure 2, D). After these early years juvenile leaves are not normally formed. However, after an injury, vigorous small trees may exhibit juvenile leaves.

Mature leaves are scale-like and completely decurrent. They are opposite on larger stems and appear to be in whorls of four on branchlets. There are two flat facial leaves which bear minute glands, the under leaf also bearing distinctive stomata bands. Facial leaves are embraced by a pair of smaller, keeled lateral leaves. As the twig elongates, lateral and facial leaves gradually separate, become more similar morphologically and eventually are opposite on the main axis (Figure 1). On these fern-like branchlets the stomata are concentrated on the underside and are marked by glaucous, patterned stomatal bands. These leaf descriptions concur with those of Laubenfels (1953), Franklin (1961), Bowers (1965) and Owens & Pharis (1971).

Branching

At the terminal, and on the laterals, new branches in western redcedar are formed one at a time, originating from stem leaf axes on alternating sides. Side branchlets arise from the axes of lateral leaves. The main stem is round in cross section and branching occurs on even numbers of leaf pairs. This sometimes forms branches in one plane, but usually the main stem twists giving the appearance of branches radiating around the main axis. The smaller, flattened branchlets twist also, orienting themselves in a horizontal plane in shade situations or vertically under sunny conditions. It is interesting to note that without these twists, western redcedar would be completely flat, lying entirely within one plane, since it branches only on lateral leaf pairs.

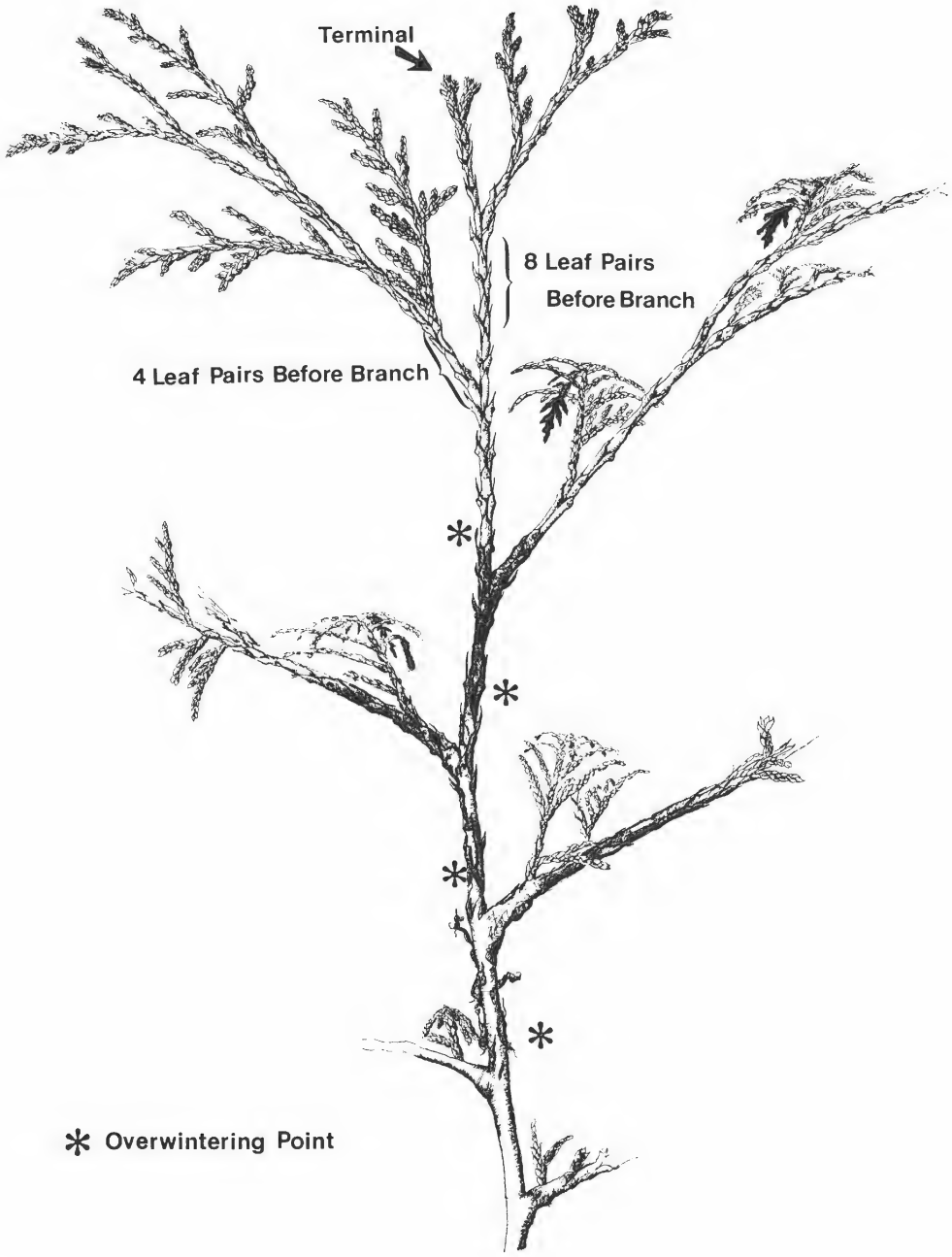

Figure 1. Branching pattern in western redcedar.

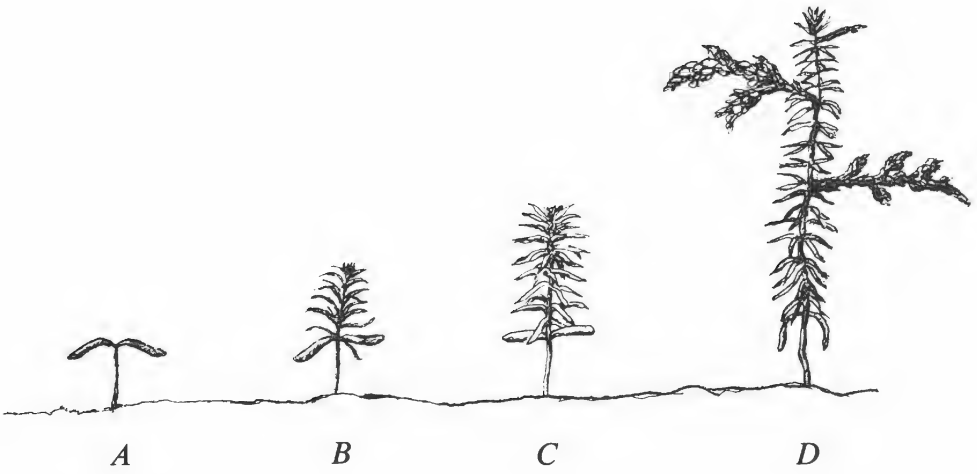

Figure 2. Seedling development in western redcedar. A-cotyledons; B,C-subulate juvenile leaves, usually ternate (B) or rarely quadrate (C); D-appearance of first mature leaves.

A terminal may produce variable numbers of branches in one growing season. We observed as many as eight branches in one year on a fast growing tree and an average of less than 0.5 branches per year on a very suppressed individual (over 28 years). Also, the distance between branches on the main stem is much less in slow growing trees than in fast growing ones. Under low light conditions lateral branches often grow longer than the terminal each year. The result is a short tree with long spindly branches. In shaded trees long branches are predisposed to being brought to the ground by gravity or litterfall and they frequently root to form vegetative clones (Habeck 1978, Parker 1979). Parker termed such individuals "veglings," along with individuals formed by other vegetative means: branches of fallen, but still rooted, trees or severed branches that root.

Locating the Terminal

The terminal apex is obvious in most conifers; not so in western redcedar. The tip of the terminal must be located to determine the height of an individual, and, if rate of growth over a season is sought, it must be located periodically. In western redcedar a developing branch is often taller than the terminal and greatly resembles it. The main stem has more leaf pairs between branches than does a lateral (Figure 1). Thus, to determine which is the terminal, count the leaf pairs on both stems of a lower fork before the next branch. The stem with the most pairs in this interval will be the main stem. Repeat this counting and comparing up the stem until the terminal is reached. Frequently the leaf pairs near the terminal are telescoped, resulting in a short main stem, often shorter than, and therefore below, a developing branch.

Determining Past Year's Height Growth

The pattern of growth in western redcedar and the resulting form make it difficult to ascertain height growth of the past. The lack of preformed shoots enable the tree to respond to climatic variables during the immediate growth season and thus may result in great differences in tree height growth in different years. Since redcedar can average from less than one branch to eight or more per year, number of branches aids little in determining a year's leader increment.

After several seasons of observing and dissecting western redcedar stems we have found reliable indicators of yearly growth cessation and resumption. Naturally, the critical location is the overwintering point. Cedar terminals normally overwinter about 1 to 2 centimeters above a branch junction (Figure 1). On the main stem, leaves expanded during different years are different in some respect. These stem leaves usually vary in color, texture or presence, separating one year's growth from the next. The color of younger leaves is more succulent and green. The texture of the remaining leaves will vary by year of origin, including the amount they have been split by the expanding stem or even the absence of leaves, with only smooth green or brown bark remaining. These year-by-year delineations are quite consistent in the majority of cases. But, in very rapidly growing trees the leaves of a season may change dramatically in their color and form, the early formed leaves being much different from the later ones. This is mainly due to the rapid swelling of the stem, splitting leaves formed early in the growing season, and making the overwintering point less obvious. Nevertheless, annual terminal increments on most individuals can be determined for the past 3 to 5 years. Slow growing trees can often be aged beyond five years.

For aging very young seedlings the stem leaves are again used, but in their juvenile form. Cotyledons normally die after the first year but remain on the seedling, providing a starting point. Yearly height growth is again told by condition of leaves.

Practice in this technique is necessary to achieve proficiency. Using a 10x hand lens and a sharp knife, several terminals on small trees should be dissected and observed. Well down the stem (about ½ to 1 meter from the terminal) cut the stem and make a ring count. An oblique cut elongates the growth rings making them easier to count. A strong light is also important. Now make a similar cross-section several branches toward the terminal and repeat the ring count. If your two dissections are the same age, they are part of the year's height growth. Keep cutting cross-sections along the stem. When two adjacent cross-sections have ring counts that vary by one year, an overwintering point, with the resulting change in stem leaves, should be visible. After some practice overwintering points on live trees will be easily recognized. Trees in the forest can then be examined and measurements made of annual growth increments without dissection.

Conclusions

Thuja plicata displays morphology common to members of the Cupressaceae. Once understood, nondestructive aging of regeneration is possible, providing quick and accurate height growth information. Such information is vital for evaluating suitability of various sites and conditions for redcedar growth.

The anatomy and growth characteristics of other members of the Cupressaceae (*Chamaecyparis, Juniperus, Libocedrus,* and other *Thuja*) resembles western redcedar, suggesting the techniques presented here may be applicable.

Acknowledgments

Funding for this project was contributed by the Research Committee and the Forest, Wildlife and Range Experiment Station, University of Idaho, with cooperation of USDA-Forest Service, Region I, and Potlatch Corporation, Lewiston, Idaho, Contribution #280, FWR Experiment Station.

Literature Cited

Aldous, J. R. and A. J. Low. 1974. The potential of western hemlock, western redcedar, grand fir and noble fir in Britain. For. Comm. Bull. No. 49.

Bowers, N. A. 1965. Cone-bearing trees of the Pacific Coast. Pacific Books, Palo Alto.

Franklin J. F. 1961. A guide to seedling identification for 25 conifers of the Pacific Northwest. USDA For. Ser. Pac. Northw. For. Range Exp. Sta., Portland, Oregon.

Habeck, J. R. 1978. A study of climax western redcedar (*Thuja plicata* Donn) forest communities in the Selway-Bitterroot Wilderness, Idaho. Northw. Sci. 52:67-76.

Kozolowski, T. T., and T. Keller. 1966. Food relations of woody plants. Bot. Rev. 32:293-382.

Laubenfels, D. J. 1953. The external morphology of coniferous leaves. Phytomorphology 3:1-20.

Mitchell, A. F. 1965. The growth in early life of the leading shoot of some conifers. Forestry 38:121-136.

Owens, J. N., and R. P. Pharis. 1971. Initiation and development of western redcedar cones in response to gibberellin induction and under natural conditions Can. J. Bot. 49:1165-1175.

Parker, T. 1979. Natural regeneration of western redcedar in northern Idaho. University of Idaho, Moscow. Thesis.

Williams, C. B., Jr. 1968. Seasonal height growth of upper slope conifers. USDA For. Ser., Pac. Northw. For. Range Exp. Sta. Research Paper PNW-62. Portland, Oregon.

Received 3 January 1986
Accepted for publication 4 March 1986.

William C. Mahaney
Geography Department, Atkinson College, York University
4700 Keele Street, North York, Ontario M3J 1P3

Tentative Growth Curve for *Rhizocarpon geographicum s. l.* in Stroud Basin, Wind River Range, Western Wyoming

Abstract

A tentative time-size curve for *Rhizocarpon geographicum s. l.* has been developed for dating Neoglacial deposits in the Wind River Range, Wyoming. Numerous differences in the maximum diameters of *R. geographicum s.l.* on Neoglacial substrates have proved useful as relative age indicators in several Wind River cirques; however, construction of a growth curve was hampered by a lack of deposits dated by radiocarbon. Using a great-growth period similar to that derived in the Front Range, Colorado, and one radiocarbon dated substrate in Stroud Basin, Wind River Mountains, a tentative curve has been constructed. *R. geographicum s.l.* appears to grow more slowly in the Wind River Mountains than in the Front Range of Colorado, the difference amounting to ~10 mm in 3000 years.

Introduction

Neoglacial sequences are common in many valleys above 3000 m in the Wind River Range in Western Wyoming. Relative age determinations of deposits have been made using topographic position, lichen and other vegetation characteristics, weathering features on surface stones, and soil morphology (Birkeland and Shroba 1974, Miller and Birkeland 1974, Mahaney 1978, 1981, 1982, 1984, Mahaney *et al.* 1984a, 1984b). Because buried organic-rich sediments are scarce, it is only rarely possible to date these deposits using radiocarbon. Moreover, since Neoglacial deposits lie above timberline, it is impossible to use tree-ring dating methods, and the absence of tephra precludes correlation and age determination by tephrachronology. In this paper a lichen growth curve for *R. geographicum s.l.* is developed which makes it possible, for the first time, to date with some accuracy the deposits in the Neoglacial sequence. After seven field seasons in the Wind River Mountains mapping deposits in four high-altitude basins, one ^{14}C dated deposit in Stroud Basin provided the necessary time-size plot required to construct a tentative curve.

Field Area

The Wind River Range is an anticlinal uplift oriented northwest-southeast and extending from South Pass to the Gros Ventre Mountains. Erosion along the eastern and western flanks of the uplift expose numerous Phanerozoic rocks (Worl 1968). A number of high-altitude basins in this range are floored with complex sequences of glacial and periglacial deposits, some of which are of Neoglacial age. Stroud Basin (Figure 1) is representative of these glaciated basins surrounded by the summits of Gannett Peak (13804 ft., 4208 m), Mount Arrowhead (12972 ft., 3954 m) and Stroud Peak (12198 ft., 3718 m). Although relatively small now, during the Neoglacial, Stroud Glacier (Figure 1) was an important valley glacier that flowed east, then north, and finally west nearly to Peak Lake. Prior to that, during the late-Pinedale, ice flowed through Stonehammer Lake Basin to the Green River.

Climate

Climatic data are summarized in Mahaney (1978) from stations along the eastern (Dubois and Lander), and western (Pinedale) flanks of the Range. The average annual temperature, mean seasonal extremes, and absolute maximum and minimum temperatures are calculated using mean winter and summer lapse rates determined in the Colorado Rockies (Barry and Chorley 1970). This gives an average annual temperature for Stroud Basin of $-3.5°$ C which is similar to values computed for the Grand Teton Glacier at 3200 m in the Teton Range, 150 km to the northwest (Mahaney 1975). The mean annual precipitation for the alpine zone is unknown, but must be significantly higher than the average snowfall reported for intermontane basin stations. The wind is predominantly northwest most of the year, and the windiest months are from October through February.

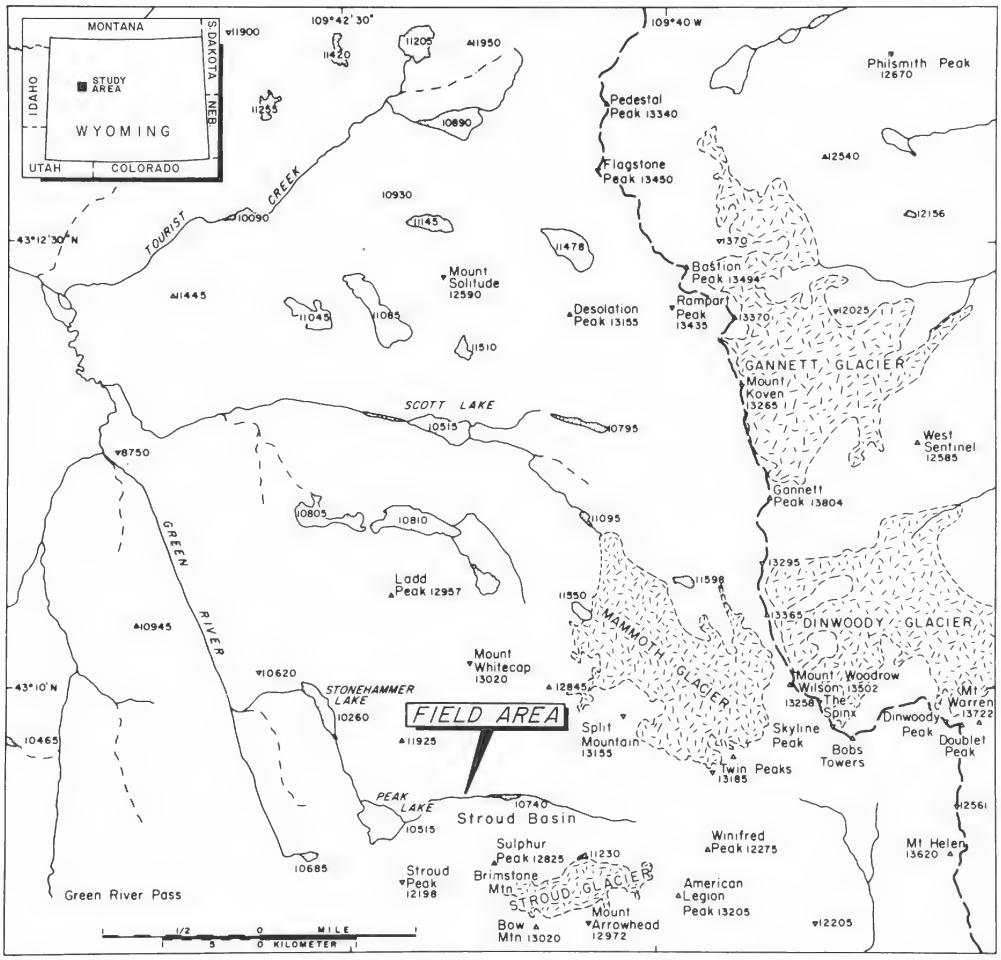

Figure 1. Stroud Basin in the central Wind River Range, Wyoming.

The alpine area is typified by short summer with cool to cold temperatures, and frequent thunderstorm activity. Winter is cold and windy with frequent cloud cover.

Precipitation regimes differ somewhat from the eastern to the western flanks of the Range (Baker 1944). On the western slope, the precipitation pattern is fairly uniform throughout the year, while on the eastern slope somewhat higher precipitation is received in May. The eastern slope is typified by a relatively higher summer rainfall than on the western slope. The Range is well-named as chinook winds descend the eastern slope toward Lander and Dubois, and are characterized by high winds. In winter months they often raise the temperature several degrees.

Vegetation

The alpine tundra, located above timberline at 3000 m, is dominated by perennial sedges, grasses, and herbaceous plants. Vegetation complexes range from kobresia meadow, dryas, and

sedge-grass, to willow-sedge stand types. The timberline zone is composed almost exclusively of whitebark pine (*Pinus albicaulis*), limber pine (*P. flexilis*), and subalpine fir (*Abies lasiocarpa*) (Reed 1976). Isolated remnants of timberline vegetation in procumbent form grow in niches sheltered from the prevailing westerly winds in the area of Peak Lake and downvalley toward Green River (Figure 1).

Methods

The principles, problems, and applications of lichenometry to geomorphological problems have been discussed by a number of workers (Beschel 1957, 1958, 1961, Benedict 1967, 1968, Curry 1969, Andrews and Webber 1964, Birkeland 1973, Birkeland and Miller 1973, Mahaney 1973, 1974, 1981, Mahaney *et al.* 1984a, 1984b, Mahaney and Spence 1984, 1985, Haines-Young 1984, 1985). The two most common assumptions employed in using lichenometry are: 1) lichen growth is indicative of elapsed time since deposition, and 2) the largest lichen thallus generally represents the oldest and fastest growing lichen on a substrate. Lichenometry may be used only for the lifespan of the lichen thallus, which is considered to be a maximum of ~3000 years for *R. geographicum s.l.* (Benedict 1967, 1968).

Deposits in Stroud and other high altitude basins were sampled with the objective of measuring the largest thalli of *R. geographicum s.l.* The measurements were made to the nearest millimeter. Only large thalli were measured and the largest of these were used to construct a tentative time-size curve. Thalli interfingering with other thalli were not measured to avoid problems with intraspecies competition. Those thalli found in depressions were not measured because snowkill might reduce the cover and impede the development of maximum diameters (Curry 1969, Mahaney 1973, 1974).

The usual restrictions adhered to by other workers of rock type, ice crystal blasting, aspect, moisture, and substrate stability were followed in this study (Mahaney 1974, 1978). All thalli were sampled on moraine crests (Figure 2) to avoid slope wash and frost creep effects. Thalli were measured on granite and granodioritic stones to minimize differences in lithology. Futher, thalli on northwest-facing boulder surfaces were not counted to avoid ice-crystal blasting effects; however, in most instances these surfaces were either devoid of lichen cover, or they contained a population with lower maximum diameters. No significant differences between maximum diameters were observed when north and south-facing aspects of boulders were compared. In all 76 lichen thalli were measured on the moraines shown in Figure 2.

The samples used for radiocarbon dating were collected from an outwash deposit described below (Figure 2) in front of the inner Indian Basin moraine in Stroud Basin at 43° 09' 30'' latitude, 109° 42' 35'' longitude. These samples were collected with metal implements, air dried on aluminum foil, and stored frozen for 10 weeks before shipment to Japan for radiocarbon dating.

Results and Discussion

Indian Basin deposits in Stroud Basin are unusually well preserved and outwash deposits can be traced to moraine fronts in the area near Peak Lake (Figure 2). Just east of Peak Lake, between an outer and inner end moraine of Indian Basin age (Mahaney 1984), an outwash deposit (STR21) emplaced 2760 ± 110 yrs BP (Gak-9597) provides a maximum age for the inner Neoglacial moraine and a minimum age for the outer moraine. The organic material in this outwash consisted of a "pocket" of detrital plant material with some old roots and intact leaf material. The surface of this deposit contained an Entisol 70 cm thick with some roots extending approximately 50 cm into the Cox horizon. The pH profile in this soil showed that H+ ion activity decreased with depth suggesting little downward movement of H^+, and hence, little contamination. Ca/Mg ion determinations show only a slight increase of Ca with depth suggesting little downward movement from the surface soil solum. Moreover, at 110 cm a ^{14}C date on plant fragments of 1960 ± 150 yrs BP (Gak-11020) suggests that some geobiochemical contamination may have occurred within the soil and upper parent material. The lower parent material showed no variations in pH or Ca/Mg ratios which would suggest that no geobiochemical contamination occurred. Therefore the date of 2760 ± 100 yrs BP appears to be a reliable age determination for the emplacement of the outwash deposit.

After sampling *all* (e.g. 48 large thalli) large thalli of *R. geographicum s.l.* on the inner and

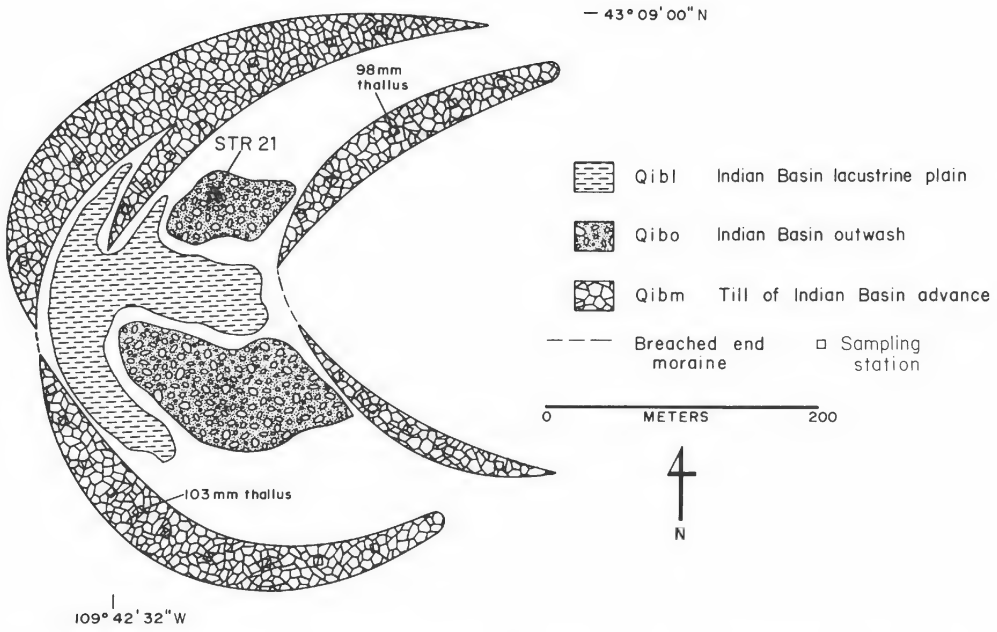

Figure 2. Indian Basin (early Neoglacial) deposits near Peak Lake, Stroud Basin, central Wind River Range, Wyoming.

outer moraine crests, the maximum diameter observed was 104 mm (Figure 3). Several other thalli gave measurements close to 100 mm, suggesting that the largest thalli was not unusually large, and that it represented the elapsed time since deposition 2760 ± 110 yrs BP. Since the cross-valley axis here is sufficiently wide (500 m), clast transport (and hence lichen transport) from the surrounding valley walls over snow banks to the moraine crest, although possible, such as in Fourth of July Cirque (Mahaney 1973), is not likely.

Having determined the maximum diameter and the age of the associated outwash deposit, it is now possible to construct a tentative growth curve for *R. geographicum s.l.* (Figure 4). The great-growth rate (defined as that occurring over the first 100 years), while not known with precision for the Wind River Range, is suspected to be similar to the Front Range in Colorado (Mahaney 1978). Assuming that the great-growth rates are similar, the differences in size after 3000 years, when compared with the Front Range, is 10 mm. The average growth per century following the great-growth period is estimated at ~3.0 mm, which is slower by 0.3 mm/century when compared with the Front Range, Colorado.

Comparing the two curves it is apparent that *R. geographicum s.l.* grows somewhat slower in the Wind River Range than in the Front Range of Colorado, apparently because it is drier there (Birkeland and Shroba 1974, Mahaney 1978, 1981). However, when making generalizations of this kind one must take into consideration that individual basins may be quite variable in the moisture available for weathering and lichen growth. Hence, further observations in the Wind River Range are needed to provide additional radiocarbon dated substrates and maximum diameters of *R. geographicum s.l.*

Conclusions

Construction of a tentative growth curve for *R. geographicum s.l.* will allow more refined dating of Neoglacial deposits in the Wind River Mountains. The initial data suggest that lichen growth (3 mm/100 yrs) is somewhat slower than in the Front Range of Colorado (3.3 mm/100 yrs),

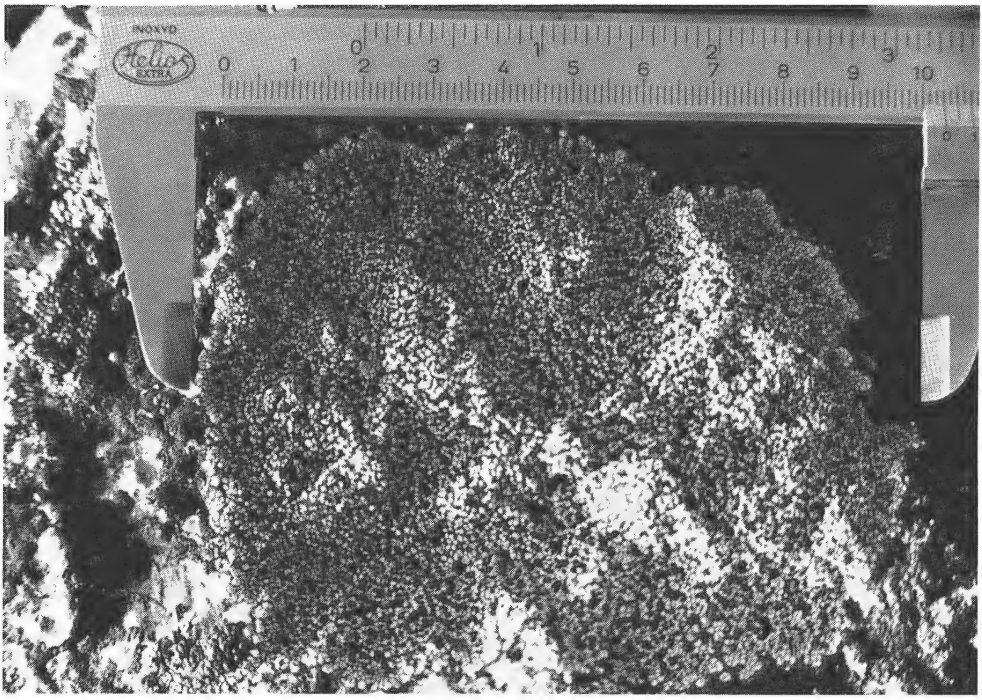

Figure 3. Thallus of *R. geographicum s.l.*, on an early Indian Basin substrate, Stroud Basin, Wind River Range, Wyoming.

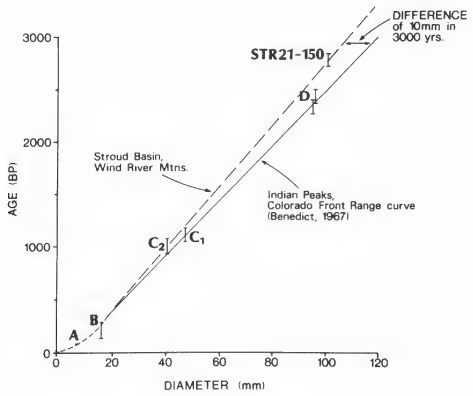

Figure 4. Tentative growth curve (dashed line) for *R. geographicum s.l.* Wind River Range, Wyoming compared with the Front Range (solid line) in Colorado (Benedict 1967; 1968). For the Colorado curve maximum lichen diameters were measured on historically dated cairns (A), debris-flow levees (B), prehistoric game-drive systems (C) and ground moraine (D) deposited at the close of the Triple Lakes (early Neoglacial) advance. The Wyoming curve is based on a similar great-growth period (Mahaney 1978) and outwash radiocarbon dated at 2760 ± 110 yrs BP. Vertical lines on all radiocarbon dates show the statistical errors.

750 km to the southeast. As more deposits are dated by radiocarbon other workers should be able to test the time-size relationships discussed herein, and refine the curve to a considerable degree.

Acknowledgements

I thank the students in York University's Mountain Geomorphology courses (1974, 1978-80) for assistance in the field. Larry Gowland helped me with some of the laboratory analyses completed in the Geomorphology and Pedology Laboratory at York University. Some inspiration for this research came from my constant companions C. and O. P. Mahaney. Research was supported by grants from York University.

Literature Cited

Andrews, J. T. and P. J. Webber. 1964. A lichenometrical study of the northwestern margin of the Barnes Ice Cap: a geomorphological technique. Geograph. Bull. 22:80-104.

Baker, F. S., 1944. Mountain climates of the western United States. Ecol. Monogr. 14:223-254.

Barry, R. G., and R. J. Chorley. 1970. Atmosphere, Weather and Climate. Holt, Rinehart, and Winston, New York.

Benedict, J. B. 1967. Recent glacial history of an alpine area in the Colorado Front Range, U.S.A. I. Establishing a lichen-growth curve. J. Glac. 6:817-832.

_____. 1968. Recent glacial history of an alpine area in the Colorado Front Range, U.S.A. II. Dating the glacial deposits. J. Glac. 7:77-87.

Beschel, R. E. 1957. A project to use lichens as indicators of climate and time. Arctic 10:60.

_____. 1958. Lichenometrical studies in West Greenland. Arctic II, 4:254.

_____. 1961. Dating rock surfaces by lichen growth and its application to glaciology and physiography (lichenometry). *In* Raasch, G. O. (ed.) Geology of the Arctic: proceedings of the first international symposium on Arctic geology, Calgary, Alberta, Jan. 11-13, 1960. Univ. Toronto Press 2:1044-62.

Birkeland, P. W., 1973: Use of relative age-dating methods in a stratigraphic study of rock glacier deposits, Mt. Sopris, Colorado. Arctic Alpine Res. 5:401-416.

Birkeland, P. W., and C. D. Miller. 1973. Reinterpretation of type Temple Lake moraine and other Neoglacial deposits, southern Wind River Mountains, Wyoming. Geol. Soc. Amer. (Abstr.) 5:465-466.

Birkeland, P. W., and R. R. Shroba. 1974. The status of the concept of Quaternary Soil-Forming Intervals in the Western U.S. *In* Mahaney, W. C. (ed.), Quaternary Environments: Proceedings of a Symposium. Geograph. Monogr. 5:241-276.

Calkin, P. E. and J. M. Ellis. 1984. Development and application of a lichenometric dating curve, Brooks Range, Alaska. *In* Mahaney, W. C. (ed.), Quaternary Dating Methods. Amsterdam: Elsevier. Pp. 227-246.

Curry, R. R. 1969. Holocene climatic and glacial history of the central Sierra Nevada, California. *In* Schumm, W. A. and Bradley, W. C., (eds.), United States Contributions to Quaternary Research. Geological Soc. Amer. Spec. Pap. 123. Boulder, Colorado. Pp. 1-47.

Haines-Young, R. H. 1983. Size variation of *Rhizocarpon* on moraine slopes in Southern Norway. Arctic Alpine Res. 15:295-305.

_____. 1985. Size variation of *Rhizocarpon* on moraine slopes in Southern Norway: Reply. Arctic Alpine Res. in press.

Mahaney, W. C. 1973. Neoglacial chronology in the Fourth of July Cirque. Central Colorado Front Range. Geol. Soc. Amer. Bull. 84:161-170.

_____. 1974. Soil Stratigraphy and genesis of Neoglacial deposits in the Arapaho and Henderson Cirques, Central Colorado Front Range. Geograph. Monogr. 5:197-240.

_____. 1975. Soils of post-Audubon age, Teton Glacier area, Wyoming. Arctic Alpine Res. 7:141-153.

_____. 1978. Late-Quaternary stratigraphy and soils in the Wind River Mountains, Western Wyoming. *In* Mahaney, W. C. (ed.) Quaternary Soils. Norwich, U.K., Geoabstracts Ltd. Pp. 223-364.

_____. 1981. Paleoclimate reconstructed from paleosols: evidence from the Rocky Mountains and East Africa. *In* Mahaney, W. C. (ed.) Quaternary Paleoclimate. Norwich, U.K., Geoabstracts Ltd. Pp. 227-247.

_____. 1982. Correlation of Quaternary glacial and periglacial deposits on Mount Kenya, East Africa with the Rocky Mountains of western U.S. XI INQUA Congress, *Abstracts,* vol. 1, U.S.S.R., Aug. 1-9, 1982. Pp. 208.

_____. 1984. Indian Basin advance: new name for early Neoglacial till in western and northcentral Wyoming. Northw. Sci. 58:94-102.

Mahaney, W. C., and J. Spence. 1984. Glacial and periglacial sequence and floristics in Jaw Cirque, Central Teton Range, western Wyoming. Amer. J. Sci. 284: 1056-1081.

Mahaney, W. C., and J. Spence. 1985. Size variation of Rhizocarpon on moraine slopes in Southern Norway: A Discussion. Arctic Alpine Res., 17(2):211-212.

Mahaney, W. C., M. G. Boyer, D. L. Halvorson, and K. Sanmugadas. 1984a. Glacial chronology of the Rocky Mountains: some problems from observations in Western Wyoming. *In* Mahaney, W. C. (ed.), Correlation of Quaternary Chronologies, Norwich, U.K., GeoBooks. Pp. 225-241.

Mahaney, W. C., J. Piegat, D. L. Halvorson, and K. Sanmugadas. 1984b. Evaluation of dating methods used to assign ages in the Wind River and Teton Ranges, Western Wyoming. *In* Mahaney, W. C. (ed.), Quaternary Dating Methods, Amsterdam, Elsevier. Pp. 355-374.

Miller, C. D. and P. W. Birkeland. 1974. Probable pre-Neoglacial age of the type Temple Lake Moraine, Wyoming: Discussion and additional relative-age data. Arctic Alpine Res. 6:301-306.

Reed, R. M. 1976. Coniferous forest habitat types of the Wind River Mountains, Wyoming. Amer. Midl. Nat. 94:159-173.

U.S. Dept. Commerce. 1965. Climatography of the U.S. No. 86-42. Climatic Summary of the U.S. Supplement for 1951-1960. Wyoming, Washington, U.S. Gov. Print. Off.

Worl, R. G. 1968. Taconite in the Wind River Mountains, Sublette County, Wyo. Preliminary Rept. No. 10. Laramie, Wyo., Geol. Survey.

Received 27 November 1985
Accepted for publication 13 May 1986

Donald B. Zobel and **Joseph A. Antos**
Department of Botany and Plant Pathology
Oregon State University, Corvallis, Oregon 97331-2902

Survival of *Veratrum viride*, a Robust Herbaceous Plant, when Buried by Volcanic Tephra

Abstract

Veratrum viride plants that survived burial by 12-18 cm of tephra from Mount St. Helens in 1980 were experimentally buried 20-50 cm deeper in 1982. Burial of dormant plants by an additional 40 cm of tephra prevented most shoot development, but only reduced survival by half when shoots were already emerging at the time of burial.

Introduction

Burial of plants by volcanic tephra elicits a variety of plant responses (Antos and Zobel 1985a, 1985b). Where tephra does not erode, buried plants must grow up through the tephra to survive. Most perennial herbs moved their underground perennating structures into the tephra, but shoots of a few species grew up through the tephra each year, retaining the original position of their overwintering buds in the buried soil. The most robust herbaceous species we encountered, and the most successful at this latter strategy, was American false hellebore, *Veratrum viride* Ait. (Liliaceae). Shoots of *V. viride,* which can exceed 2 m tall when flowering, pushed up through 15 to 18 cm of tephra, including a hard 1 cm surface crust, with no evident difficulty.

The purpose of the experiments described here was to determine how deep a tephra deposit would be required to prevent the emergence of shoots of *Veratrum viride.*

Study Area and Methods

A *Veratrum viride* population was chosen at 1200 m elevation, 22 km NE of Mount St. Helens, Washington, in an area covered by 12-18 cm of tephra on 18 May 1980 (described by Antos and Zobel 1985b). The plants grew among scattered *Abies amabilis, Tsuga mertensiana,* and *Alnus sinuata.* They showed no adverse effects of the 1980 eruption at the time they were chosen in 1982.

Experiment 1. On 30 June 1982, six clumps were chosen with 3 to 5 shoots each just emerging (0-15 cm tall) from the tephra. Two clumps were randomly assigned to each treatment, treatments being 20, 30, or 40 cm of additional burial. Clumps were buried by shoveling tephra from the surrounding area carefully over the shoots. Emergent shoots were counted, measured, and checked for damage on 15 September 1982, 14 September 1983, and 5 September 1984. On the last sampling date, all mounds were excavated and the buried parts of all shoots measured and examined.

Experiment 2. On 15 September 1982, ten additional clumps with 3-6 shoots each were chosen, and shoot heights measured. Clumps were assigned randomly to one of two treatments, of 40 and 50 cm additional burial, and buried on 1 October 1982, after the shoots had died. Observations were made in 1983-4 as for Experiment 1.

Experiment 3. Four mounds from Experiment 2 with no emerging shoots were excavated 14 September 1983. Shoots were measured and then reburied to 30 cm deeper than natural tephra. Observations were made in 1984 as in Experiment 1.

The experiment terminated when the stand was logged late in 1984.

Results

Shoot Emergence from Tephra

Aerial shoots developed from all clumps buried in Experiment 1 (Table 1). All shoots visible at burial grew through 20 cm of added tephra (as did several shoots not visible at burial), but about half failed to escape burial by 30 and 40 cm. In 1983 and 1984, shoots emerged from the same points as 1982 shoots, presumably following the same path through the mound.

The ten clumps buried in the fall after shoot senescence (Experiment 2) produced 43 shoots

TABLE 1. Experiment 1: Responses of shoots buried by 20, 30, and 40 cm tephra after emergence from the natural tephra in June 1982. Values in parentheses are standard deviations. Measurements were all in September except the "before" shoot number.

Burial Depth (cm)	Actual Depth (cm)	Number of shoots				No. Flowering			Shoot Heights (cm)			No. Leaves
		before	1982	1983	1984	1982	1983	1984	1982	1983	1984	1984
20	33.0 (1.4)	7	11	12	11	0	2	0	45 (9)	67 (31)	65 (9)	9.0 (2.1)
30	38.5 (2.1)	8	3	4	3	0	1	0	31 (15)	67 (47)	55 (19)	9.0 (2.5)
40	48.0 (1.4)	10	5	5	8	0	3	0	37 (11)	110 (59)	45 (23)	6.5 (2.1)

the season before burial. After burial only one clump, buried by 40 cm, produced emergent shoots, two in 1983 and three in 1984. No shoots emerged in 1984 from four clumps reburied less deeply in 1983 (Experiment 3).

Shoot Size and Flowering

The shallowest burial produced the tallest shoots in 1982 and 1984 (Table 1) but differences were non-significant. Shoots buried the deepest had significantly fewer leaves in 1984 (leaves were not counted in 1983). In 1983, flowering occurred but did not appear to be related to depth of burial (Table 1). In 1984, however, no experimental shoots produced flowers; in contrast, about 40 percent of unburied shoots near the experiment flowered.

Damage to Emergent Shoots

In 1982, all leaves of shoots emerging from 40 cm deep burial were torn, except for the top two leaves on 2 of the 5 shoots; in contrast, those buried with 20 cm of tephra had only slight abrasion damage on the lower leaves. Plants buried 30 cm had intermediate levels of leaf damage. Damage to deeply buried shoots was less in later years.

Condition of Buried Shoots

Excavation in September 1984 revealed only one buried shoot that had not emerged from the six tephra mounds in Experiment 1. In contrast, the ten clumps buried in the fall had 32 buried shoots, averaging 16 to 37 cm long (except for clump 15 at 59 cm). Since total tephra depth was 40 to 68 cm, most shoots were too short to emerge even if they had grown straight up. In clump 15, one shoot grew nearly to the surface and then downward, and another grew twisted through the mound.

There was no difference in buried shoot length among the treatments in Experiments 2 and 3 in 1984, nor any significant correlation between length of buried shoots and shoot height of the clump before burial. Buried shoots were significantly taller in 1984 than in 1983 in the four mounds excavated both years (31 *vs.* 14.5 cm).

All buried shoots were abraded and dying back from the tip, which was often rotten. In 1983, most buried shoot tissue was dead in mid-September. Shoots usually grew vertically near the base but bent or twisted farther into the mounds. Shoots lost vigor as they grew into the mound, the apical parts being of much smaller diameter than below.

Almost all emergent shoots grew vertically, their buried length equal to (or for a few up to 3 cm greater than) the depth of the tephra. Many followed the same route through the mound as shoots of previous years.

Discussion

Veratrum viride copes more successfully with burial after shoots begin growth in the spring than with burial while plants are dormant. Forty cm of additional tephra was fatal to most shoots when dormant, but to only half those buried while shoots were growing. The difference may result because, in the spring, the emergent shoots are closer to the surface, tissue is "hardened" by exposure at the time of burial, and the tephra is less compact. In subsequent years, spring-buried

shoots face the same problems as fall-buried ones, except that there are pathways through the mound followed by shoots the year before.

The effect of burial appears to occur after shoots begin growth. Leaf abrasion and tearing appeared to be caused by friction as the shoots pushed up through the coarse, rough tephra. Gas exchange beneath the tephra potentially could be a problem, but with the loose, coarse tephra in the mounds, and the initial vigorous vertical growth, it seems unlikely to be important here. Reduced gas exchange is more likely to be critical in a natural deep tephra deposit, however. There, deep tephra would not be in isolated mounds, and the fine layers as produced from the 1980 eruption (Waitt and Dzurisin 1981) would be intact, offering a more effective barrier to gas exchange.

The 1980 tephra deposit was shallow enough to allow most or all *Veratrum viride* to survive, although it eliminated all except isolated individuals of other forest herbs near the study area (Antos and Zobel 1985c). Earlier deposits in the area have been substantially deeper (Waitt and Dzurisin 1981). A deposit twice as deep, falling on dormant plants, could kill most *V. viride.* If *Veratrum* shoots were above the soil, still in the compact form in which they penetrate it, the effect would probably be much less severe. The shoots retain this less susceptible form, however, for only about two weeks. When the leaves are spread, as during most of the growing season, damage is again likely to be great; the weight of even a few mm of fallen tephra trapped in the expanded leaves toppled shoots of *Veratrum californicum* (Mack 1981). Except when flowering, the aerial "stem" of *Veratrum viride* is composed only of concentric, elongated, sheath-like leaf bases, with the meristem remaining below ground. Thus the plant may be more susceptible to toppling or abrasion damage than shoots of a similar size that include stem tissue. Even so, its very large size and robust shoots give *Veratrum* an advantage over most other species.

The effect of tephra on a particular organism or other natural system varies drastically with the condition of that system (for example, see Antos and Zobel 1982). In our case, *Veratrum,* singled out as being particularly vulnerable to falling tephra while mature (Mack 1981), proved to be the herb best able to cope with burial of its perennial organs by much deeper tephra, in areas where shoots had not yet developed.

Literature Cited

Antos, J. A. and D. B. Zobel. 1982. Snowpack modification of volcanic tephra effects on forest understory plants near Mount St. Helens. Ecology 63:1969-1972.

_____. 1985a. Plant form, developmental plasticity, and survival following burial by volcanic tephra. Can. J. Bot. 63:2083-2090.

_____. 1985b. Upward movement of underground plant parts into deposits of tephra from Mount St. Helens. Can. J. Bot. 63:2091-2096.

_____. 1985c. Recovery of forest understories buried by tephra from Mount St. Helens. Vegetatio 64:103-111.

Mack, R. N. 1981. Initial effects of ashfall from Mount St. Helens on vegetation in eastern Washington and adjacent Idaho. Science 213:537-539.

Waitt, R. B. Jr. and D. Dzurisin. 1981. Proximal air-fall deposits from the May 18 eruption—Stratigraphy and field sedimentology. *In* Lipman, P. W. and D. R. Mullineaux (ed.) The 1980 Eruption of Mount St. Helens, Washington. U.S. Geol. Survey Prof. Paper 1250. Pp. 601-616.

Received 20 September 1985
Accepted for publication 2 May 1986

Thomas P. Sullivan and **John A. Krebs,** Applied Mammal Research Institute
23523 47th Avenue R. R. #7, Langley, B.C., Canada V3A 4R1

and

H. Anthony Kluge, Crop Protection Branch, Ministry of Agriculture and Food
Parliament Buildings, Victoria, B.C., Canada V8V 1X5

Survey of Mammal Damage to Tree Fruit Orchards in the Okanagan Valley of British Columbia

Abstract

This study reports on the incidence of damage from vole, pocket gopher, and deer that feed on tree fruit orchards in the Okanagan Valley of British Columbia, Canada. A secondary objective was assessment of the relative use of various techniques for control of this mammal damage. An on-site sampling survey of 10% of orchardists recorded the intensity of damage with respect to fruit species as well as age and size of a given orchard. Rodent and deer damage, based on tree mortality or reduced growth and yield, was reported for more than 30% and 24% of the orchards, respectively. Some fruit production districts had 10% of orchards with severe (> 10%) losses from deer browsing. Young (< 10 years old) apple orchards, 8 ha or more in area were highly susceptible to damage by pocket gophers, voles, and deer. Soil texture had little effect on incidence of vole or pocket gopher attack. Toxicants were the most widely-used technique for reducing rodent populations. Fencing was the only reliable means of preventing deer browsing in orchards. Commercial deer repellents often provided inconsistent and unreliable protection for fruit trees.

Introduction

The Okanagan Valley produces most of the tree fruits and grapes in British Columbia. Prime agricultural land in this region occupies valley bottoms, low elevation benchlands, and southern-exposure slopes. Several mammal species native to the Okanagan interact with tree fruit production in this area.

Three species of voles, *Microtus montanus* (montane), *M. pennsylvanicus* (meadow), and *M. longicaudus* (long-tailed) reside within or adjacent to fruit orchards. Voles inflict serious feeding damage by barking and girdling trees during the winter season (Anderson 1980). The northern pocket gopher (*Thomomys talpoides*), a fossorial geomyid, is found in the subterranean orchard environment. Pocket gophers damage fruit trees by feeding on roots and underground bark and this damage may occur year-round (Anderson 1980). The negative impact of bark and associated vascular tissue removal on tree vigour and fruit yield has been clearly illustrated for apple orchards in New York state and related areas of the eastern United States (Pearson and Forshey 1978).

Rocky mountain mule deer (*Odocoileus hemionus hemionus*) are abundant in the Okanagan Valley. Northwest white-tailed deer (*O. virginianus ochrourus*) and Rocky Mountain elk (*Cervus elaphus nelsoni*) are also found in some areas of the Valley. Deer and elk traditionally migrate from high elevation summer ranges to low elevation, southern exposure winter ranges. The proximity, and in many cases overlap, of prime agricultural land and preferred winter range has resulted in serious browsing and antler rubbing damage to fruit trees by deer and elk. Newly planted trees and high-density plantings of semi-dwarf trees are particularly vulnerable to wild ungulate damage.

Intensive control programs (Byers *et al.* 1976) and surveys (Anthony and Fisher 1977) of mammal damage to orchards have been conducted in the eastern United States. However, there is virtually no information available on the extent and severity of mammal damage to tree fruit orchards in the Okanagan Valley. Thus, this study was designed to investigate the incidence of vole, pocket gopher, and deer damage to orchards in the Okanagan, and determine the relative use of various techniques for control of mammal damage.

Materials and Methods

An on-site sampling survey of 195 orchardists in the five tree fruit production districts of the Okanagan Valley (Fig. 1) was conducted during

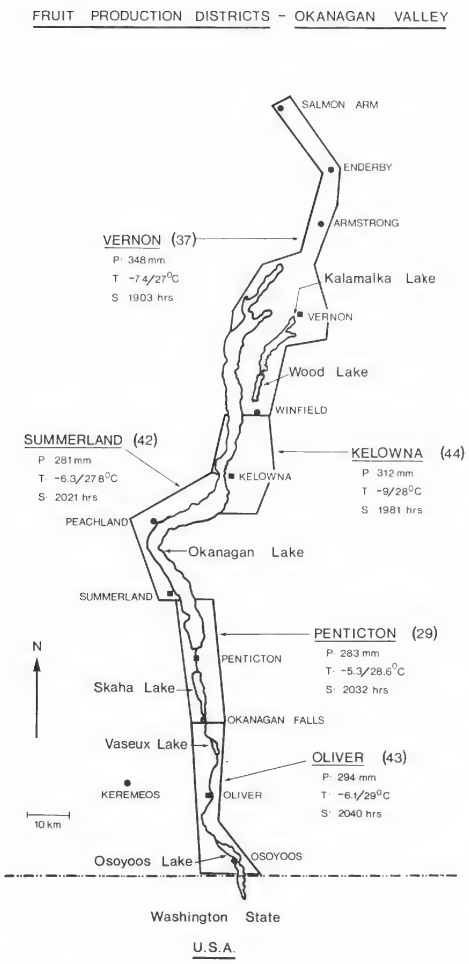

Figure 1. Map of study area showing the five fruit production districts, number of orchards sampled in parentheses, and climatic data: average annual precipitation (P), hours of sunshine (S), and average low (January) and high (July) temperatures (T).

May to August 1983. From a composite list of 2000 to 2200 growers, every tenth grower was selected for an interview. The number of orchards sampled in each district reflected the abundance of tree fruit growers in that area.

The species and variety, age of trees and area (ha) were recorded for each orchard. In many cases, an individual grower had several species (e.g. apple, cherry, apricot) and ages of trees in blocks within the overall orchard. In terms of rodent habitat, soil texture was assessed on a scale of 1 to 6 (1 = clay, 2 = clay/loam, 3 = silt/loam, 4 = sand/loam, 5 = sand/gravel, 6 = clay/gravel). Vole and pocket gopher feeding damage to trees during the last five years was recorded as none, light (< 1% loss), moderate (1 to 10% loss) or severe (> 10% loss). Tree loss may be interpreted as mortality or reduction in growth and yield. Assessment of control techniques for voles included the proportion of growers using cultural practices (mowing between tree rows with herbicide along rows), poison baits (toxicants), and tree guards (wire mesh or plastic). For pocket gophers, techniques included trapping, poison placed in burrows, and use of an artificial burrow builder with poison bait. Browsing damage by deer and elk was recorded in the same manner as rodent damage. Control techniques included fencing, repellents, shooting, and various scare devices (including domestic dogs). Results from the survey are summarized according to the five fruit production districts in the Okanagan Valley (Fig. 1).

Results

Climate

Average annual precipitation and hours of sunshine as well as average low (January) and high (July) temperatures for each district in the Okanagan Valley are given in Fig. 1. A slight degree of cooling (1.6° to 2°C) and increase in precipitation (53 mm) occurs from south to north (Oliver to Vernon). However, there is generally little variation in these data with the general climate classified as semi-arid.

Rodent Damage

The incidence of damage by voles and gophers in each district during the last 5 years is illustrated in Fig. 2A. The Oliver district had significantly fewer orchards with pocket gopher damage than any of the other districts. Similarly, Oliver had significantly fewer orchards with vole damage than Vernon. The incidence of vole and pocket gopher damage was generally comparable in the Penticton to Vernon districts ranging from 31.8% to 40.5%. Overall, 2.6% of orchards had moderate and 1.5% had severe tree mortality

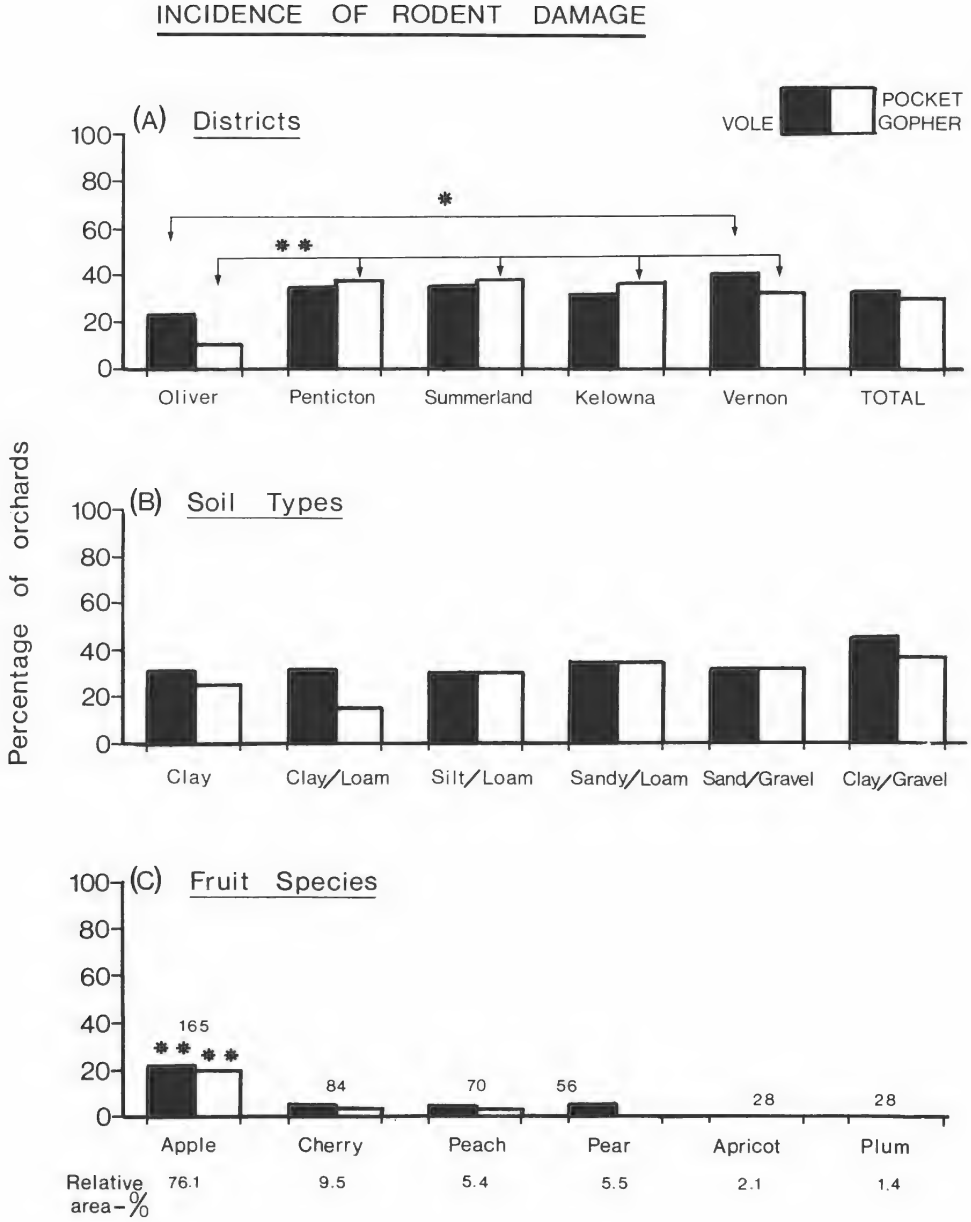

Figure 2. Percentage of orchards with feeding damage by voles and pocket gophers in: (A) five fruit production districts; (B) various soil types; and (C) various fruit tree species. * $p < 0.05$, ** $p < 0.01$; significant difference by chi-square.

from vole attack. These attack rates were 2.1% and 0.5% respectively, for gophers.

To determine if soil texture limits the distribution of voles, and particularly pocket gophers, this variable was related to the incidence of damage (Fig. 2B). Except for the clay/loam soil type which had fewer ($p = 0.058$, chi-square) orchards with pocket gopher damage than the sand/loam type, soil texture appeared to have little effect on supporting vole and pocket gopher populations in an orchard environment.

Assessment of which species of fruit trees were attacked by voles and pocket gophers is illustrated in Fig. 2C. Apple trees were readily attacked by these rodents with more than five times as many apple orchards with damage compared with cherry and peach. It should be stressed that apple orchards (76.1% of production area) dominate the Okanagan Valley and this may in part explain their higher frequency of attack than the other fruit species.

In general, voles and pocket gophers attacked young (1- to 10-year-old) fruit trees in all districts with totals of 75.9% and 92.9%, respectively. In terms of size, large orchards were more susceptible to vole ($r = 0.93$, $n = 6$; $p < 0.01$) and pocket gopher ($r = 0.98$, $n = 6$; $p < 0.01$) damage than small orchards (Figs. 3A and 3B). There was little difference in the percentage of orchards with vole damage between the 4- and 8-ha size classes. Orchards > 12 ha had comparable vole damage (52.2%) to that in the 8.1-12 ha class (total of 56.3%) and these classes combined had significantly ($p < 0.01$, chi-square) more damage than those orchards < 8 ha in area. Pocket gopher damage to orchards increased significantly from the 4- to 8-ha classes at Vernon and overall ($p < 0.01$; chi-square). In a similar manner to vole damage, pocket gopher feeding (36.5% overall) increased significantly ($p < 0.01$; chi-square) from the 8- to 12-ha class (75% overall). However, damage declined ($p < 0.05$; chi-square) to 43.5% in orchards > 12 ha.

In summary, vole populations occupied and damaged approximately 30% of all orchards up to 8 ha and 54% of orchards > 8 ha in area. Pocket gopher populations damaged more trees in large than small orchards up to 12 ha in area.

The percentages of growers using various types of control measures for rodent damage are presented in Table 1. Cultural practices involving grass mowing and herbicide treatments along tree rows were used by 83.8% of growers overall (range of 76.7 to 90.0%). The main function of these practices is to reduce vegetative competition, thereby enhancing tree growth and yield. They are considered to be of secondary importance for controlling vole damage at the present time. However, experimentation with mowing and herbicides as a means of habitat manipulation may provide significant reduction of vole and pocket gopher populations.

The use of acute and/or anti-coagulant poison baits to reduce vole populations was the most common and widespread control technique. More than one-third of growers used poison with particularly heavy use in the Summerland (45.2%) and Kelowna (50.0%) districts. The proportion of growers with damage who use poison but continued to have a problem with voles was 54.2% (39/72). This measurement reflects the generally poor long-term efficacy of poison in suppressing vole populations. Conversely, the proportion of growers who did not have a damage problem but still used poison was 45.8% (33/72). Tree guards were used by 9.2% of growers.

Poison was also the major technique employed by growers to reduce pocket gopher populations and damage (Table 1). Nearly one-half (48.7%) of all orchards had baits placed in gopher burrows either by hand-probe injection or by mechanical burrow builder. Penticton and Summerland districts had particularly high user rates for pocket gopher poison (62.1% and 66.7%, respectively). Oliver had the lowest use at 25.6% which corresponds with their significantly low incidence of pocket gopher damage (see Fig. 2A). However, 46.3% (44/95) of those growers using poison continued to have damage. This also tends to reflect the inability of poison to maintain pocket gopher populations at a consistently low level in the orchard environment. The proportion of growers without a damage problem but who still used poison in pocket gopher burrows was 53.7% (51/95). Kill-traps were used by 27.2% of growers overall and 32.1% of these also used poison. The burrow builder was used in 10.8% of orchards and was usually accompanied by hand-probe placement of poison. Only 13.3% of orchards had both vole and pocket gopher damage.

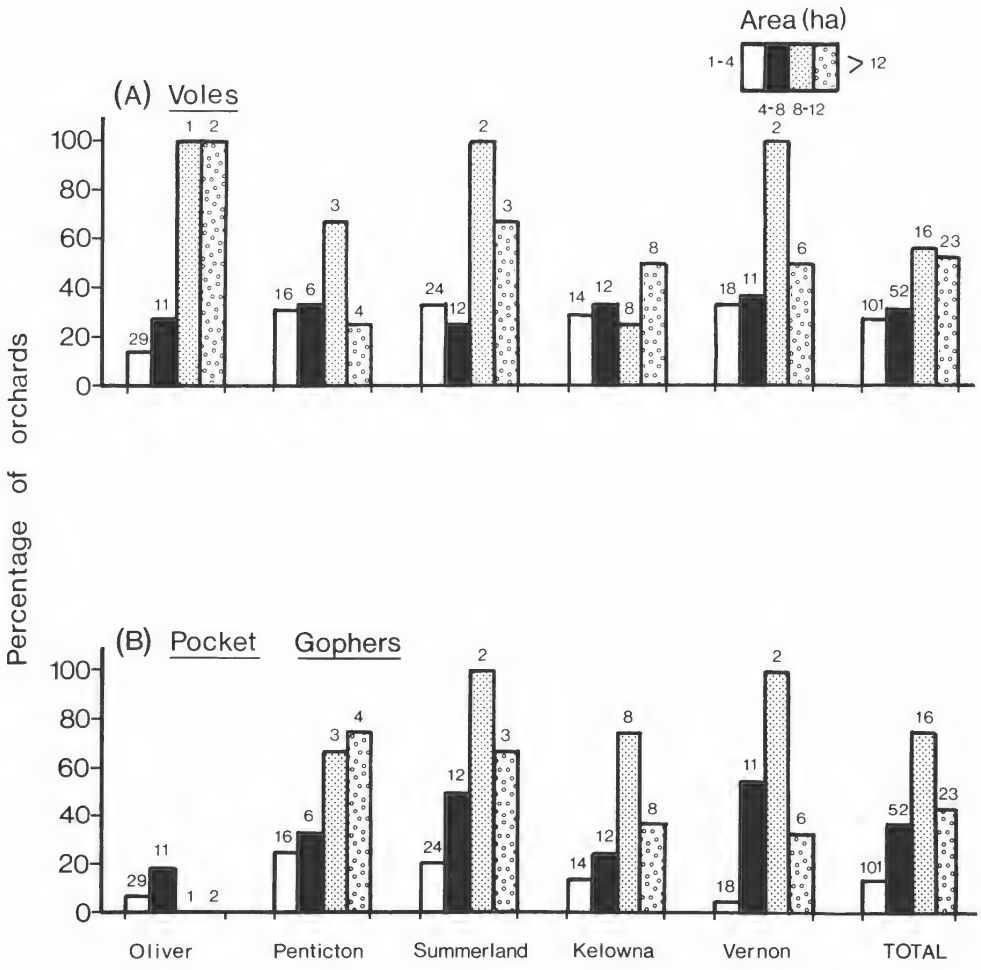

Figure 3. Percentage of orchards with (A) vole and (B) pocket gopher feeding damage in four size classes for the five fruit production districts. Sample size above each histogram.

Deer Damage

The incidence of browsing damage by deer in each district is illustrated in Fig. 4A. The Oliver district had significantly fewer orchards with deer damage than in Penticton, Summerland, or Vernon. In addition, Kelowna district (18.2%) had fewer orchards with browsing damage relative to Penticton (41.4%). All districts except Oliver had orchards with serious tree damage or loss (> 10%). This was particularly evident in Penticton (10.3%) and Vernon (10.8%). A total of 6.2% of orchards had serious damage from antler rubbing (Harder 1970) on young trees.

TABLE 1. Percentage of growers using various types of control measures for rodent damage to orchards in the Okanagan Valley. Proportion of growers with damage who use poison but still have a problem is indicated in parentheses. a-a, b-b, c-c, d-d, $p < 0.05$; e-e, f-f, g-g, $p < 0.01$; significant difference by chi-square.

Control measures	District					Total
	Oliver	Penticton	Summerland	Kelowna	Vernon	
Voles						
Cultural practices	85.3	90.0	77.8	87.5	76.7	83.8
Poison baits	25.6[a] (5/11)	27.6 (4/8)	45.2 (9/19)	50.0[a] (13/22)	32.4 (8/12)	36.9 (39/72)
Tree guards	2.3	10.3	11.9	9.1	13.5	9.2
Pocket Gophers						
Poison baits	25.6[bef] (1/11)[cdg]	62.1[e] (10/18)[c]	66.7[f] (13/28)[d]	47.7[g] (13/21)	45.9 (7/17)	48.7 (44/95)
Traps	20.9	20.7	30.9	36.4	24.3	27.2
Burrow builder	4.7	3.4	11.9	13.6	18.9	10.8

The incidence of damage by deer to the various fruit species is illustrated in Fig. 4B. Deer attacked apple trees (19.4%) more readily than cherry (5.9%) or other fruit trees (0.0%). As with the selection for different trees by voles and pocket gophers, apples are the major crop in the Okanagan and this factor may have some influence on the lack of feeding damage to other fruit tree species.

Young (1- to 5-year old) trees (73.1%) were particularly susceptible to deer attack. Ninety-six percent of all deer-damaged trees were < 15 years old.

Large orchards were generally more susceptible to deer browsing ($r = 0.97$, $n = 7$; $p < 0.01$) than small orchards (Fig. 4C). In specific districts, orchard damage from deer declined in the > 12 ha size class in Summerland and Vernon, and was the same as the 8.1-12 ha class in Kelowna. Overall, orchards > 8 ha had significantly ($p < 0.01$; chi-square) more browsing than those < 8 ha in area.

The percentages of growers using various types of control measures for deer damage are presented in Table 2. Fencing of orchards was highest (20.7%) in the Penticton district which is predictable based on the levels of serious browsing (Fig. 4A). The total percentage of orchards with fencing was 7.2%. Repellents, both commercial and home-made, ranged from 2.3% use in Oliver to 16.7% in Kelowna. Use of shooting and scare devices ranged from 0% to 4.8%. Those growers using repellents were generally dissatisfied with efficacy.

Discussion

Our data clearly substantiate the detrimental effects of mammal damage to orchards as viewed by commercial orchardists. These results are comparable to those from other studies (McDowell and Pillsbury 1959, Anthony and Fisher 1977). Although moderate to severe damage (based on tree loss and reduced growth and yield) levels were generally low (< 3%) among the approximately 30% of growers with feeding injuries from voles and pocket gophers, any degree of tree replacement on an annual or multi-annual basis can have a significant economic impact. Laidlaw (1982) has provided a cost-benefit analysis of the potential dollar value of tree loss in orchards and its importance to orchard management. Severe (> 10%) losses to deer browsing are clearly of great significance to a given grower in terms of current and future production loss and tree replacement.

The consistency in vole and pocket gopher damage through the various districts from Oliver to Vernon is not surprising if the low variation in climatic parameters and intensive orchard irrigation and cultivation methods are considered.

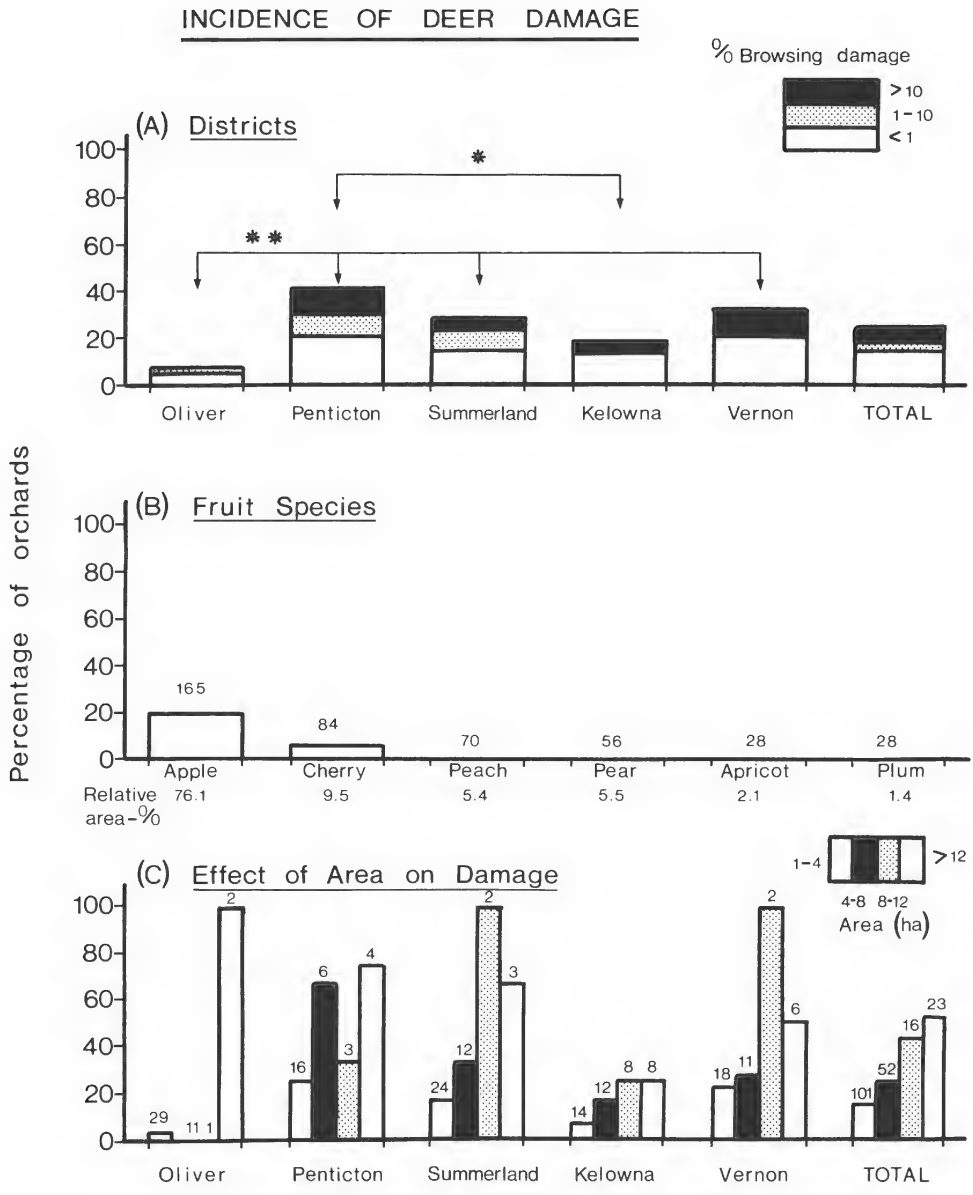

Figure 4. Percentage of orchards with feeding damage by deer in: (A) five fruit production districts; (B) various fruit tree species; and (C) four size classes (sample size above each histogram). * $p < 0.05$, ** $p < 0.01$; significant difference by chi-square.

TABLE 2. Percentage of growers using various types of control measures for deer damage to orchards in the Okanagan Valley. a-a, b-b, c-c, $p < 0.05$; d-d, $p < 0.01$; significant difference by chi-square.

Control measures	District					Total
	Oliver	Penticton	Summerland	Kelowna	Vernon	
Fencing	4.7[a]	20.7[abd]	9.5	4.5[b]	0.0[d]	7.2
Repellents	2.3[c]	10.3	16.7[c]	11.4	8.1	9.7
Shooting	2.3	3.4	4.8	2.3	2.7	3.1
Scare devices	2.3	3.4	4.8	2.3	0.0	2.6

In an essentially dry climate, irrigated orchards in Vernon, Summerland, and Oliver are likely to provide productive grassland/forb habitat for voles and pocket gophers as well as excellent winter forage for deer. Our assessment of soil texture and distribution of rodent damage indicated little difference among the various soil types. Pocket gophers and the semi-fossorial pine vole (*M. pinetorum*) of eastern North America are known to have specific soil requirements (Miller 1964, Best 1973, Fisher and Anthony 1980). Thus, the lack of soil preference by either voles or pocket gophers in the Okanagan may be a result of the irrigation and fertilization regimes which make the orchard environment attractive regardless of soil texture. This explanation is further supported by studies of pocket gopher activity in natural habitats where sandy soils are clearly preferred to those with clay-dominated soils (T. P. Sullivan, unpublished). Soil texture would not be a reliable criterion upon which to base a control program since location of new orchards on certain soils may not reduce pocket gopher damage.

The low proportion (13.3%) of orchards with both vole and pocket gopher damage suggests that each rodent has specific requirements to occupy an orchard habitat and maintain a population level high enough to result in feeding attacks to trees. These requirements could not be identified on the basis of our survey. However, neither species showed a "preference" for a given fruit species (other than apple) or for soil type. Other factors which might be important include distance from natural habitats which may act as source areas for rodents to colonize orchards.

The Oliver district had the most intensive and widespread area of available land in fruit production and this may explain the lower incidence of rodent damage in that area. The quality and quantity of grass species with respect to food and cover in orchard blocks and the relative proportions of herbs, forbs, and grasses may influence the distribution and abundance of voles and pocket gophers, respectively (Ward and Keith 1962, Thompson 1965; Vaughan 1967, Grant and Morris 1971, Birney *et al.* 1976).

Unfortunately, orchards which appear to be particularly susceptible to mammal damage cover a wide range of situations in the Okanagan Valley where there has been a trend towards producing more compact fruit trees. High-density plantings of semi-dwarf trees are commonly found in new orchards, interplantings, and orchard renovations (replacement). These tree are especially sensitive to deer and elk damage during the early nonproductive years when careful pruning and shaping is essential for maximum production in later years. In addition, they will remain vulnerable to mammal damage throughout most of their productive years.

Toxicants are widely used to control vole and pocket gopher populations in the Okanagan Valley. However, their efficacy was uncertain because approximately 50% of all growers using toxicants continued to have damage problems. In these cases, the use of poison for the purpose of population reduction provides only short-term success in controlling rodent damage. In addition, many growers without rodent damage continue to use poison baits even though their use may not be required in many orchard situations.

Intensive study of the population dynamics of voles and pocket gophers is essential to the development of successful control techniques. The existence of multi-annual and annual

fluctuations in vole abundance makes predictability of feeding damage difficult. An integrated control strategy could reduce or eliminate damage more effectively than the widespread use of toxicants. Intensive studies in this direction are presently being conducted in the Okanagan Valley.

Deer damage is clearly of the greatest significance to growers at the present time. A substantial effort is now being made to rehabilitate winter range in the Okanagan Valley. This is a sound management approach to damage reduction but it must be coupled with specific protection for orchards which continue to attract deer.

Permanent fencing, either conventional or electric, can be installed to physically exclude deer from orchards. Conventional woven (page) wire fencing is prohibitively expensive in most cases. High-tensile, high-voltage electric fencing has been demonstrated to be an effective and economical alternative to conventional fencing. However, many growers may prefer the option of applying a chemical repellent to provide temporary protection for fruit trees during times of heavy deer pressure.

Commercial repellents have been developed with little regard for their biological significance to deer or durability in the field. It is not surprising that the vast majority of growers find commercially available repellents to be ineffective. A reliable repellent system with biologically significant origins such as predator odours (Melchiors and Leslie 1985, Sullivan *et al.* 1985) released from a weather-proof dispenser is urgently needed.

Acknowledgements

We thank Agriculture Canada and the Applied Mammal Research Institute for financial support and B.C. Ministry of Agriculture and Food for logistical support services. We are grateful to D. S. Sullivan for much of the data organization and preparation of figures, and to E. J. Hogue for review of the manuscript.

Literature Cited

Anderson, G. G. 1980. Rodent control on agricultural land in British Columbia. B.C. Min. Agric. Publ. 80-6.

Anthony, R. G., and A. R. Fisher. 1977. Wildlife damage in orchards—A need for better management. Wildl. Soc. Bull. 5:107-112.

Best, T. L. 1973. Ecological separation of three genera of pocket gophers (Geomyidae). Ecology 54:1311-1319.

Birney, E. C., W. E. Grant, and D. D. Baird. 1976. Importance of vegetative cover to cycles of *Microtus* populations. Ecology 57:1043-1051.

Byers, R. E., R. S. Young, and R. D. Neely. 1976. Review of cultural and other control methods for reducing pine vole populations in apple orchards. Proc. 7th Vertebrate Pest Conference. Monterey, California. Pp. 242-253.

Fisher, A. R., and R. G. Anthony. 1980. The effect of soil texture on distribution of pine voles in Pennsylvania orchards. Amer. Midl. Nat. 104:39-46.

Grant, P. R., and R. D. Morris. 1971. The distribution of *Microtus pennsylvanicus* within grassland habitat. Can. J. Zool. 49:1043-1052.

Harder, J. D. 1970. Evaluating winter deer use of orchards in western Colorado. Trans. N. Amer. Wildl. Conf. 35:35-47.

Laidlaw, G. W. J. 1982. The potential dollar value of tree loss in orchards. Proc. 5th Great Plains Wildlife Damage Control Workshop. Lincoln, Nebraska. Pp. 69-70.

McDowell, R. D., and H. W. Pillsbury. 1959. Wildlife damage to crops in the United States. J. Wildl. Manage. 23:240-241.

Melchiors, M. A., and C. A. Leslie. 1985. Effectiveness of predator fecal odors as black-tailed deer repellents. J. Wildl. Manage. 49:358-362.

Miller, R. S. 1964. Ecology and distribution of pocket gophers (Geomyidae) in Colorado. Ecology 45:256-272.

Pearson, K., and C. G. Forshey. 1978. Effects of pine vole damage on tree vigor and fruit yield in New York apple orchards. HortScience 13:56-57.

Sullivan, T. P., L. O. Nordstrom, and D. S. Sullivan. 1985. The use of predator odours as repellents to reduce feeding damage by herbivores. II. Black-tailed deer (*Odocoileus hemionus columbianus*). J. Chem. Ecol. 11:921-935.

Thompson, D. Q. 1965. Food preferences of the meadow vole (*Microtus pennsylvanicus*) in relation to habitat affinities. Amer. Midl. Nat. 74:76-86.

Vaughan, T. A. 1967. Food habits of the northern pocket gopher on shortgrass prairie. Amer. Midl. Nat. 77:176-189.

Ward, A. L., and J. O. Keith. 1962. Feeding habits of pocket gophers on mountain grasslands, Black Mesa, Colorado. Ecology 43:744-749.

Received 18 December 1985
Accepted for publication 12 June 1986

Wayne A. Hubert, Wyoming Cooperative Fishery and Wildlife Research Unit
University of Wyoming, Laramie, Wyoming 82071

and

George T. Baxter and **Mark Harrington,** Department of Zoology and Physiology
University of Wyoming, Laramie, Wyoming 82071

Comparison of Age Determinations Based on Scales, Otoliths and Fin Rays for Cutthroat Trout from Yellowstone Lake

Abstract

Ages determined from scales, otoliths, dorsal fin rays, and pectoral fin rays of a sample of Yellowstone Lake cutthroat trout (*Salmo clarki*) were compared. The four structures yielded similar precision between separate readings by a single observer. Discrepancies in age determinations between scales and the other structures were observed. Otoliths tended to yield older ages than scales, whereas fin rays tended to yield ages similar to or lower than those based on scales. The use of scales may lead to an aging bias that results from the failure of some fish to form scales during their first year of life.

Introduction

The use of scales to age fish began in the late 19th-century and is now widely applied for aging cutthroat trout, Salmo *clarki.* Scales have been used to age cutthroat trout from Yellowstone Lake, Yellowstone National Park, since management of the lake was initiated in the late 1940's (Laakso and Cope 1956, Bulkley 1961, Benson and Bulkley 1963), but fishery biologists have not been satisfied with the precision of estimates based on scale readings. This study was initiated in an attempt to find a more satisfactory method for age assessment.

Recent research has indicated that other structures may provide more precise estimators of age among slow-growing, soft-rayed, freshwater fishes. Because the most promising structures appeared to be otoliths and fin ray sections, we selected them for assessment and comparison with scales in this study.

Otoliths have been used to estimate the age of brook trout, *Salvelinus fontinalis* (Reimers 1979); Arctic grayling, *Thymallus arcticus* (Sikstrom 1983); lake whitefish, *Coregonus clupeaformis* (Barnes and Power 1984); round whitefish, *Prosopium cylindraceum* (Jessop 1982); cisco or lake herring, *Coregonus artedii* (Morin 1980); and longnose sucker, *Catostomus catostomus* (Tripp and McCart 1974). In general, few differences between ages determined from scales and from otoliths have been observed among young fish, but estimates based on otoliths were consistently older than those based on scales for older fish.

Fin ray sections have been used to age brown trout, *Salmo trutta* (Burnet 1969); Arctic grayling (Sikstrom 1983); lake whitefish (Mills and Beamish 1980); and white sucker, *Catostomus commersoni* (MacCrimmon 1979). Like otoliths, fin ray sections have tended to yield older age estimates than scales among older fish. Burnet (1969) found that two observers correctly read scales from only 6 of 29 known-age brown trout, whereas Burnet correctly read fin ray sections from all of 22 known-age brown trout.

On the basis of the results of previous studies with otoliths, dorsal fin ray sections, and pectoral fin ray sections, we selected these structures to determine if they would yield better precision than scales in aging Yellowstone Lake cutthroat trout. We assessed the precision of age estimates between independent readings of the same structure by one observer, as well as the precision of age estimates among the four structures based on age determinations derived from readings by three observers.

Methods

Cutthroat trout were obtained during the annual gill-netting assessment of Yellowstone Lake fish stocks by the U.S. Fish and Wildlife Service, on September 18, 1984. Scales, dorsal fins, and right pectoral fins were removed in the field, stored in individually coded envelopes, and returned to the laboratory for preparation and aging. Scales were scraped with a knife from above the lateral line near the dorsal fin. Fins were cut at the base

with surgical scissors. Otoliths were removed through the roof of the mouth, after gills and the isthmus had been removed to expose the ventral surface of the cranium. The otoliths were removed with forceps, and placed in individual glass vials containing 70% ethanol.

Scale preparation closely followed the procedure of Hagenbuck (1970). A wet mount of several scales was made on a microscope slide and one scale showing clear annuli was photographed. Dorsal and pectoral fins were embedded in epoxy and sectioned (0.7-0.9 mm thick) with a microstructural cutting saw. Cross sections were mounted on a microscope slide with Permount, one to two drops of xylene, and a cover slip; then examined under a dissecting microscope. Otoliths were placed in anise oil for four to six weeks (Reimers 1979). Cleared otoliths were placed on microscope slides with a drop of toluene to remove the anise oil residue, and were examined under a dissecting microscope, utilizing reflected light (Mosher and Eckles 1954).

Annuli on scales were identified according to the techniques of Lux (1971). We relied on only the presence of discontinuous or broken circuli to identify annular marks. When otoliths were observed, layers making up spring and summer growth appeared as white, opaque bands, and layers laid down during fall and winter appeared as dark, translucent bands (Lux 1971). Similar zonation patterns were observed on fin-ray sections. The first annulus was difficult to identify in many fin-ray sections.

Two independent age determinations (the reader did not know the results of the previous reading) were made on each structure by one technician who had been trained in annulus identification, to determine the precision among readings by one observer.

One reading of each structure was conducted independently by each of two additional technicians. The first reading by the three technicians was used as the estimate of fish age. When two or three of the readings agreed, this value was accepted as the correct age. When no two readings agreed, the median value was accepted as the age.

Results were analyzed by determining the percent agreement among independent readings of a structure by one technician, as well as among age determinations when different structures were used. Chi-square analysis was used to determine significant trends. The "Index of Average Percent Error" (AEI%) of Beamish and Fournier (1981) was computed for all comparisons.

Results

Reader Agreement

Percent agreement of age determination between two independent readings ranged from 51% with otoliths to 72% with pectoral fin rays (Table 1). The AEI% ranged from 15% for scales to 33% for otoliths. Precision between readings was the poorest for otoliths and the best for scales and pectoral fin rays.

A comparison of the number of agreements and disagreements among the four structures, made by using a 2 x 4 Chi-square contingency table, yielded a significant difference in the ratio of agreements to disagreements (Chi-square = 12.557, df = 3, $p < 0.01$). When the same comparison was made without otoliths, no significant difference in the ratio of agreements to disagreements was observed. These results indicated that the agreement between first and second readings was similar among the structures, except for otoliths which produced a higher level of disagreement.

Age determinations based on the two independent readings differed by as much as three years (Table 1). Age determinations differed by one year in 26% of the pectoral fin ray readings, and in 35% of the otolith readings.

Comparisons of Age Determinations

Agreement between age determinations was lowest (51%) for the comparisons between otoliths and fin ray sections and highest (56%) between scales and all three of the other structures (Table 2). A 2 x 6 Chi-square contingency test of the number of agreements and disagreements in age determination among the six comparisons of structures indicated no significant difference among the structures. This test indicated that no two structures yielded a higher level of aging precision than any of the others.

The AEI%, computed for the six comparisons of aging precision among the four structures (Table 2), ranged from 22% for scales and pectoral fin ray sections to 28% for otoliths and pectoral fin ray sections.

TABLE 1. Results of two independent age determinations by a trained technician using four different structures from Yellowstone Lake cutthroat trout.

Structure	Sample size	Percent agreement	Percent disagreement by different numbers of years			AEI%[a]
			One	Two	Three	
Scales	110	72	26	2	0	15
Otoliths	107	51	35	10	3	33
Dorsal fin rays	108	68	29	2	2	19
Pectoral fin rays	108	72	26	1	1	15

[a]See text for explanation.

TABLE 2. Percent agreement between age determinations based on four different structures from Yellowstone Lake cutthroat trout. The index of average percent error (AEI%) is in parentheses.

Structure	Structure Compared		
	Scales	Otoliths	Dorsal Fin Rays
Otoliths	56 (26)		
Dorsal fin rays	56 (24)	51 (27)	
Pectoral fin rays	56 (22)	51 (28)	54 (23)

Bias in age determination among the four structures was indicated (Figure 1). When scales were compared to the other structures, scales tended to yield lower ages than otoliths (figure 1a), to have about the same aging bias as dorsal fin rays (Figure 1b), and to yield higher ages than pectoral fin rays (Figure 1c). Otoliths tended to yield higher age determinations than either dorsal fin rays or pectoral fin rays (Figure 1d, e). When dorsal fin ray age determinations were compared to those of pectoral fin rays, it was observed that dorsal fin rays tended to yield higher age determinations (Figure 1f).

Discussion

The results of this study disagreed with recent literature indicating that the use of scales for aging slow-growing fishes may be a less desirable choice than otoliths or fin ray sections. Differences in the life span of Yellowstone Lake cutthroat trout compared with that of fish in other stocks that were studied may contribute to the disagreement. The Yellowstone Lake cutthroat trout in our sample were from one to six years old. Samples used in other studies included fish with a life span more than twice that of Yellowstone Lake cutthroat trout. Differences in age determinations tended to appear among fish older than six years in the other studies (Beamish and Harvey 1969, Beamish and Chilton 1977, Power 1978, Sikstrom 1983, Barnes and Power 1984).

Discrepancies in age determinations between scales and other structures may be partly due to the frequent failure of Yellowstone Lake cutthroat trout to grow large enough to form scales during their first year of life (Laakso 1955). The only structure to show a trend toward older age determination was the otolith. Fin rays tended to yield age determinations similar to, or less than, those given by scales. This tendency may be due to the difficulty in identifying the first annulus in fin ray cross sections (Beamish 1973).

Otoliths tended to yield older age determinations than sections of either pectoral or dorsal fin rays. This tendency may be further evidence that the first annulus was not being identified on many of the fin ray cross sections.

The results of this study indicated that aging precision was not high with any structure studied, and otolith and fin ray cross sections did not yield better precision in age determinations of Yellowstone Lake cutthroat trout than scales. However, the data indicated that the use of otoliths may reduce some aging bias that occurs when using only scales. Age estimates may be

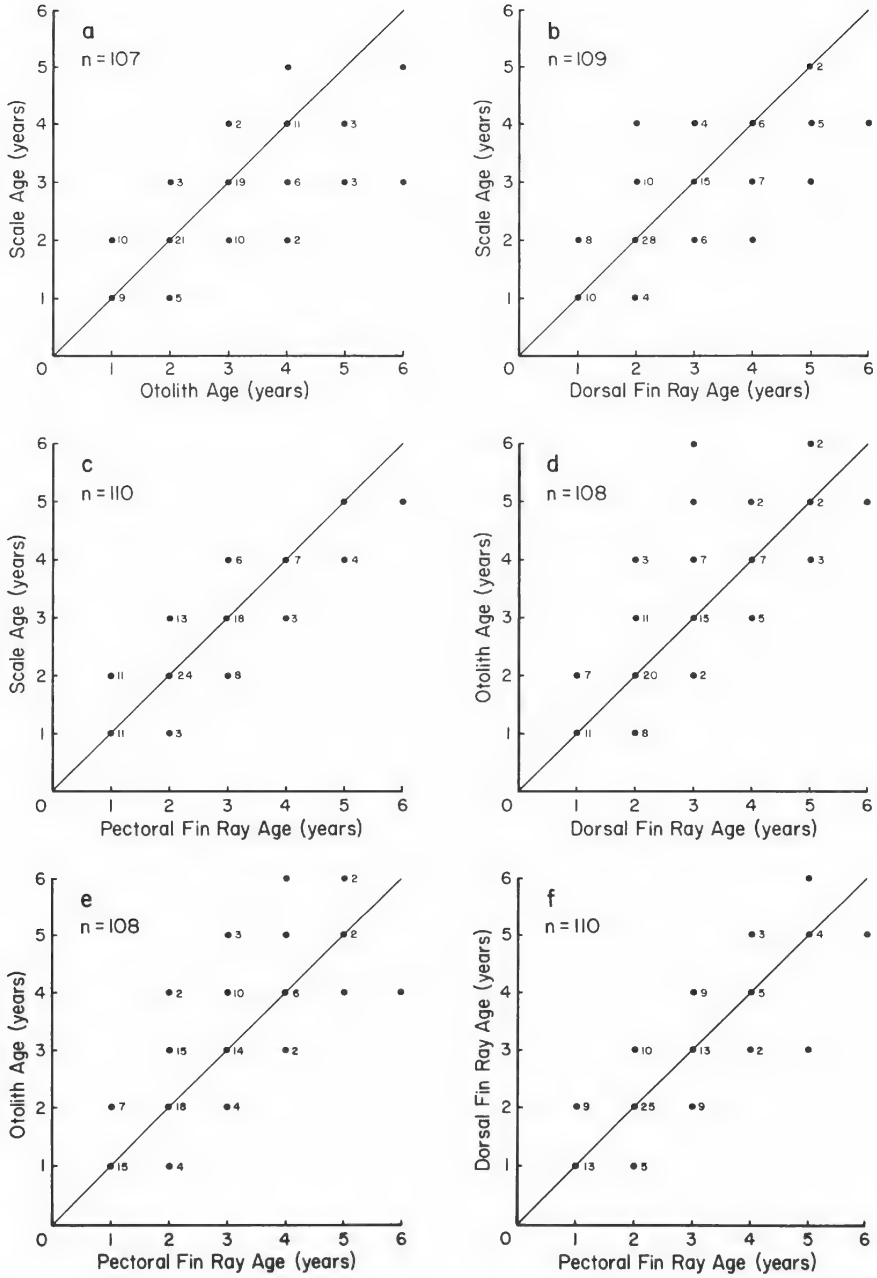

Figure 1. Comparisons of age determinations based on scales, otoliths, dorsal fin rays, and pectoral fin rays for Yellowstone Lake cutthroat trout. Points are individual fish except where indicated by a number. Points on diagonal line indicate comparisons where assigned ages by both structures were identical.

more accurate if scales and otoliths are used in combination. When the techniques described are used, otoliths are easy to remove from fish in the field and to prepare and read in the laboratory. We believe that the use of both scales and otoliths for aging Yellowstone Lake cutthroat trout should be considered.

Beamish and McFarlane (1983) cautioned fishery workers to validate age and growth studies by using mark-recapture experiments or assessment of known-age fish from a population. Such a validation has not been done on Yellowstone Lake cutthroat trout and would be difficult because both the lake and the population are large. They suggested that if validation studies are not possible, fish should be aged by several methods, and the possibility of errors in age estimates be considered. Our study provided a basis for suggesting that the use of one or two additional methods for determining the age of cutthroat trout would improve aging techniques currently used at Yellowstone Lake.

Acknowledgments

We appreciate the assistance of the U.S. Fish and Wildlife Service's Yellowstone Fishery Assistance Project Crew—specifically Ronald Jones, Robert Gresswell, and Leo Lentsch. David Gulley provided field help and Eric Featherston provided laboratory assistance. The study was supported by the University of Wyoming—National Park Service Research Center. The Wildlife Research Unit is supported by the University of Wyoming, the Wyoming Game and Fish Department, the Wildlife Management Institute, and the U.S. Fish and Wildlife Service.

Literature Cited

Barnes, M. A. and G. Power. 1984. A comparison of otolith and scale ages for western Labrador lake whitefish, *Coregonus clupeaformis*. Environ. Biol. Fish. 10:297-299.

Beamish, R. J. 1973. Determination of age and growth of populations of the white sucker (*Catostomus commersoni*) exhibiting a wide range in size at maturity. J. Fish. Res. Board Can. 30:607-616.

Beamish, R. J., and D. Chilton. 1977. Age determination of lingcod (*Ophiodon elongatus*) using dorsal fin rays and scales. J. Fish. Res. Board Can. 34:1305-1313.

Beamish, R. J., and D. A. Fournier. 1981. A method for comparing the precision of a set of age determinations. Can. J. Fish. Aquat. Sci. 38:982-983.

Beamish, R. J., and H. H. Harvey, 1969. Age determination in the white sucker. J. Fish. Res. Board Can. 26:633-638.

Beamish, R. J., and G. A. McFarlane. 1983. The forgotten requirement for age validation in fisheries biology. Tran. Amer. Fish. Soc. 112:735-743.

Benson, M. G. and R. V. Bulkley. 1963. Equilibrium yield and management of cutthroat trout in Yellowstone Lake. U.S. Fish Wildl. Serv. Res. Rep. 66.

Bulkley, R. V. 1961. Fluctuations in age composition and growth rate of cutthroat trout in Yellowstone Lake. U.S. Fish Wildl. Serv. Res. Rep. 54.

Burnet, A. M. R. 1969. An examination of the use of scales and fin rays for age determination of brown trout (*Salmo trutta* L.). New Zealand J. Mar. Freshwat. Res. 3:147-151.

Hagenbuck, W. W. 1970. A study of the age growth of the cutthroat trout from the Snake River, Teton County, Wyoming. University of Wyoming, Laramie. Thesis.

Jessop, B. M. 1972. Aging round whitefish (*Prosopium cylindraceum*) of the Leaf River, Ungava, Quebec, by otoliths. J. Fish. Res. Board Can. 29:452-454.

Laakso, M. 1955. Variability in scales of cutthroat trout in mountain lakes. Proc. Utah Acad. Sci. Arts Let. 32:81-87.

Laakso, M. and O. B. Cope. 1956. Age determination in Yellowstone cutthroat trout by the scale method. J. Wildl. Manage. 20:138-153.

Lux, F. E. 1971. Age determination of fishes (Revised). U.S. Natl. Mar. Fish. Serv. Fish. Leafl. 637.

MacCrimmon, H. R. 1979. Comparative annulus formation on anatomical structures of the white sucker, *Catostomus commersoni* (Lacepede). J. Fish. Manage. 10:123-127.

Mills, K. H. and R. J. Beamish. 1980. Comparison of fin ray and scale age determination for lake whitefish (*Coregonus clupeaformis*) and their implications for estimates of growth and annual survival. Can. J. Fish. Aquat. Sci. 37:534-544.

Morin, R. 1980. Ecology of anadromous coregonine fishes in estuaries of eastern James-Hudson Bay. Laval University, Quebec. Thesis.

Mosher, K. H., and H. H. Eckles. 1954. Age determination of Pacific sardines from otoliths. U.S. Fish Wildl. Serv. Res. Rep. 37.

Power, G. 1978. Fish population structure in arctic lakes. J. Fish. Res. Board Can. 35:53-59.

Reimers, N. 1979. A history of a stunted brook trout population in an alpine lake: a lifespan of 24 years. Calif. Fish Game 65:196-215.

Sikstrom, C. B. 1983. Otolith, pectoral fin ray, and scale age determinations for Arctic grayling. Prog. Fish-Cult. 45:220-223.

Tripp, D. B., and P. J. McCart. 1974. Life histories of grayling (*Thymallus arcticus*) and longnose suckers (*Catostomus catostomus*) in the Donnelly River system, Northwest Territories. *In* Canadian Arctic Gas Study Limited. Biological Report Series. Vol. 20, Chap. 1.

Received 3 January 1986
Accepted for publication 29 May 1986

Donald R. Johnson, Department of Biological Sciences
University of Idaho, Moscow, Idaho 83843

Effect of Alternative Tillage Systems on Rodent Density in the Palouse Region

Abstract

Social behavior and seasonal breeding regulate the numbers of deer mice (*Peromyscus maniculatus*) below that causing significant damage to grain crops under both conventional and conservation tillage systems in the Palouse region. Montane vole (*Microtus montanus*) populations are regulated through social behavior, variation in the length of the breeding season and changes in vegetative cover. Local populations of this species demonstrate both multi-year and annual patterns of density change. At higher densities voles cause damage to grain crops irrespective of the tillage system in effect, particularly where crops adjoin uncultivated shrub-grassland.

Introduction

Alternative forms of tillage are being adopted in the Palouse region to reduce erosion, soil moisture loss and energy costs. In one method, termed "no-till," the seed is drilled directly into residue of the preceding crop, thus eliminating the need to prepare a seed bed by conventional plowing. Herbicides are used to control weeds and fertilizers are applied as necessary to improve yields. Among its unfavorable effects, conservation tillage delays maturation of the crop due to insulative effects of residues and establishes a microenvironment favorable to insect pests and plant diseases (Papendick and Miller 1977; Phillips *et al.* 1980). Although rodents "thrive" in corn under conservation tillage (Johnson *et al.* 1985), their response to conservation tillage of winter wheat has not been investigated. Here I report population levels of deer mice and voles at sites under alternative methods of tillage and compare vole numbers in winter wheat cropland with that in adjoining shrub-grassland.

Methods

Abundance of deer mice was monitored using Museum Special traps baited with rolled oats and peanut butter and set out at 3 m intervals in transects of 50-200 traps. Trap lines were maintained 1-2 days at 7 locations in Whitman County, Washington, and Latah County, Idaho, in 1980 and 1981. During 1983-85, I monitored vole density at Waha, Nez Perce County, Idaho, using a 4 x 9 grid of pitfall traps (Boostra and Krebs 1978) with 12.3 m (40 ft) spacing in an uncultivated shrub-grass site. In 1985 vole abundance was concurrently monitored in adjoining cropland under conservation tillage and chemical fallow (2 transect lines of 9 pitfall traps with 12.3 m spacing in each). Pitfall traps were prebaited with rolled oats for one day and activated for 1-3 days between April and October at 2-week (1983) or monthly intervals (1984 and 1985). Snowfall prevented sampling in October, 1985. Cotton batting was provided to reduce mortality. Voles were weighed, toe-clipped and released at the site of capture.

The abundance of deer mice is reported as N/100 trap-days. I have not analyzed these data statistically because the trapping sites were arbitrarily chosen (treatments were not randomly assigned). The abundance of montane voles is reported as minimum number alive (MNA) where MNA is the sum of animals captured at time t and those assumed to be present based on their capture both previous and subsequent to t. To equalize trapping effort on the grid and transect lines, I compared the number of voles captured on the outer lines of the grid with the number captured on paired transect lines at other sites. Thus each sample represents captures on transect lines of 9 pitfall traps each with the lines spaced at least 36 m apart.

Results

Deer mice occurred in low to moderate numbers (1-34/100 trap days) in winter wheat under conventional and conservation tillage at the sites sampled during the spring and summer months, 1980 and 1981 (Table 1). Since site and treatment (tillage method) are confounded, I cannot attribute the differences observed to treatment

TABLE 1. Capture rates (N/100 trap-days) of deer mice at conventional and conservation tillage sites, 1980 and 1981. — Not trapped.

Month/	Idaho Sites		Washington Sites	
Year	Conventional	Conservation	Conventional	Conservation
April 1980	10	6.5	2.7	11
May	10	4.3	7.5	16.5
May-June	8	3	4	7.5
June	7	4.5	5	6.5
June-July	5	10	2	7
July-August	6	1	0	—
September	9	—	2	3
Sept-October	6.5	3	0	4.5
May 1981	—	—	12.5	14.4
May-June	4	4	27.5	34

alone. However, the values reported represent indices of density at these locations. Small numbers of house mice (*Mus musculus*), vagrant shrews (*Sorex vagrans*) and western jumping mice (*Zapus princeps*) were captured at sites under both tillage systems.

The montane vole population in uncultivated shrub-grassland at Waha demonstrated an annual spring peak in numbers during 1983-85 (Fig. 1). Temporary decreases in population size due to application of a zinc phosphide rodenticide in 1983 will be presented elsewhere. The differences in peak numbers between years were nearly identical to a density index of voles captured in drift fences at Coyote Grade, Nez Perce County (Fig. 2), an indication of local synchrony in density change. In 1985 the peak number of voles in shrub-grass was twice that in chemical fallow where cropping was postponed and weeds were controlled with herbicides. No voles were captured in a wheat field under conservation tillage during the summer months (Fig. 3).

DISCUSSION

Although deer mouse populations occasionally reach high densities, (e.g. Hoffmann 1955), their numbers are regulated below an economic threshold through territoriality and winter breeding rarely occurs (Metzgar 1980). The large numbers of deer mice (43/100 trap days) captured in wheat stubble near Pullman, Washington, in November, 1983 (D. Johnson, unpubl.) and in

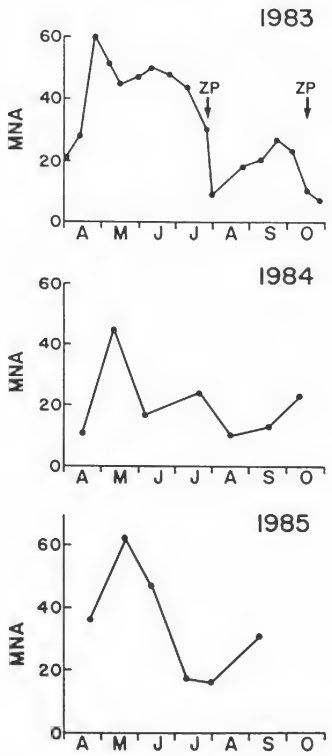

Figure 1. Minimum number of montane voles alive (MNA) on a 0.35 ha grid of pitfall traps at Waha, Nez Perce County, Idaho 1983-85. ZP—application of pelletized zinc phosphide rodenticide.

barley stubble in an earlier study (Janulewicz 1971), probably represent a response to an increased availability of waste grain. These high-density populations steadily decline during the winter months when breeding is suspended.

Birney *et al.* (1976) have confirmed that voles increase in density and establish a multiyear cycle at sites with sufficient grass cover on the Great Plains. Since both montane and long-tailed voles (*Microtus longicaudus*) demonstrate a 3-4 year cycle of density change in uncultivated Palouse grassland (Randall and Johnson 1979), one would expect periodic damage to adjoining crops. This however did not occur at the Waha site where the population fluctuated in an annual rather than multiyear pattern (Fig. 1).

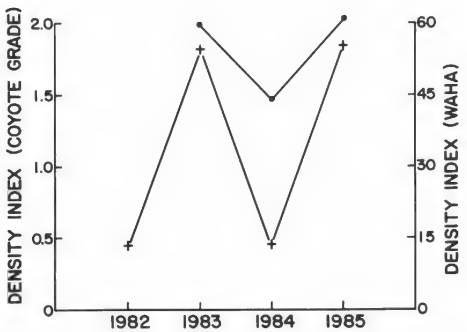

Figure 2. Density indices of montane vole populations, Nez Perce County, Idaho: Waha (.) based on minimum number alive in May (this study) and Coyote Grade (+) based on number of voles captured/30 m drift fence/ 100 trap-days (R. L. Wallace and L. V. Diller, pers. comm.).

The factors inducing cyclic change in vole density are much disputed despite extensive efforts to identify them (Meserve and Klatt 1985). In the West, the most severe irruptions of montane voles occur in large, interior basins allotted to forage crops, especially alfalfa (Murray 1965). Voles caused significant damage to seedling winter wheat under both conventional and conservation tillage at Waha in November, 1981, particularly where cropland adjoined uncultivated ground (R. Lloyd, pers. comm.).

Montane voles are capable of reproduction during the winter months if phytoestrogenic compounds are available in green forage (Negus *et al.* 1977). The social biology of montane voles is complex with females demonstrating intra-sexual

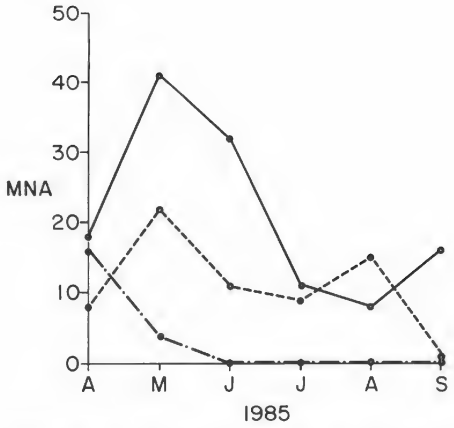

Figure 3. Minimum number of montane voles alive (MNA) in shrub-grass (solid line), chemical fallow (dashed line) and no-tillage winter wheat (dot-dash line) at Waha, Nez Perce County, Idaho, 1985. MNA in shrub-grass is adjusted to reflect trapping effort equivalent to that at the other locations.

territoriality. Their territories overlap those of adult males. Only territorial males are sexually mature in high density populations. Females form extended maternal families at high densities and the sexual maturation of young associated with these families is delayed (Jannett 1984). Thus the regulation of montane vole populations is complex, making prediction of density change difficult.

The impact of voles on grain crops has received limited attention. Citing earlier work, Ryszkowski *et al.* (1973) reported that European voles can cause serious damage to seedling wheat which sometimes results int he loss of the entire crop. Based on estimates of food requirements and density, Grodzinski *et al.* (1977) concluded that voles had little impact on winter wheat during "normal" years and only 2-3% of the crop was destroyed during periods of high density. Unfortunately, these estimates of total impact (food plus wastage) did not include the fall and winter months when voles are mostly like to cause damage to grain crops.

Acknowledgements

I thank Robert Crabtree, Kevin Moore, Philip Hall and Harry McCarty for field assistance. Richard Lloyd and 6 other Palouse farmers

encouraged this work and provided access to sites under different tillage systems. R. L. Wallace and L. V. Diller shared unpublished data regarding vole density at Coyote Grade. I also thank E. L. Michalson for his cooperation and encouragement. This study was funded through a STEEP grant to the University of Idaho from the U.S. Department of Agriculture.

Literature Cited

Birney, E. C., W. E. Grant, and D. D. Baird. 1976. Importance of vegetative cover to cycles of *Microtus* populations. Ecology 57:1043-1051.

Boonstra, R. and C. J. Krebs 1978. Pitfall trapping of *Microtus townsendii.* J. Mammal. 59:136-148.

Grodzinki, W., M. Makomaska, R. Tertil, and J. Weiner. 1977. Bioenergetics and total impact of vole populations. Oikos 29:494-510.

Hoffmann, R. S. 1955. A population-high for *Peromyscus maniculatus.* J. Mammal. 36:571-572.

Jannett, F. W., Jr. 1984. Reproduction of the montane vole, *Microtus montanus,* in subnivean populations. Carnegie Mus. Nat. Hist. Special Publ. 10:215-224.

Janulewicz, R. D. 1971. Small mammal populations in Palouse croplands. M.S. Thesis, University of Idaho.

Johnson, R. J., A. E. Koehler, O. C. Burnside, and S. R. Lowry. 1985. Response of thirteen-lined ground squirrels to repellents and implications for conservation tillage. Wildl. Soc. Bull. 13:317-324.

Meserve, P. L., and B. J. Klatt. 1985. Evidence for noncycling populations and the importance of immigration in voles inhabiting an Illinois tallgrass prairie. Amer. Midland Nat. 113:255-270.

Metzgar, L. H. 1980. Dispersion and numbers in *Peromyscus* populations. Amer. Midland Nat. 103:26-31.

Murray, K. F. 1965. Population changes during the 1957-58 vole (*Microtus*) outbreak in California. Ecology 46:163-171.

Negus, N. C., P. J. Berger, and L. G. Forslund. 1977. Reproductive strategy of *Microtus montanus.* J. Mammal. 58:347-353.

Papendick, R. I., and D. E. Miller. 1977. Conservation tillage in the Pacific Northwest. J. Soil and Water Conservation 32:49-56.

Phillips, R. E., R. L. Blevins, G. W. Thomas, W. W. Frye, and S. H. Phillips. 1980. No-tillage agriculture. Science 208:1108-1113.

Randall, J. A., and R. E. Johnson. 1979. Population densities and habitat occupancy by *Microtus longicaudus* and *M. montanus.* J. Mammal. 60:217-219.

Ryszkowski, L., J. Goszczynski, and J. Truszkowski. 1973. Trophic relationships of the common vole in cultivated fields. Acta Theriol. 18:125-165.

Received 10 February 1986
Accepted for publication 2 April 1986

Leslie Kline, 301 S. Lex Springmill Rd.
Mansfield, OH 44906

and

Bruce McCune, Holcomb Research Institute
Butler University, Indianapolis, IN 46208

Factors Influencing the Distribution of *Wolffia columbiana* and *Wolffia punctata* (Lemnaceae)

Abstract

In the Mission Valley of western Montana, prairie potholes containing *Wolffia punctata* Griseb. and *W. columbiana* Karst. were compared to nearby potholes lacking these species. Potholes without *Wolffia* had a significantly higher conductivity and pH and a lower maximum depth than those with *Wolffia. Elodea* spp. and *Lemna minor* L. were positively associated with *Wolffia.* The dependence of *Wolffia*'s distribution on environmental conditions suggests that local dispersal limitations are less important than environmental limitations in controlling the distribution of *Wolffia.*

Introduction

Wolffia species (Lemnaceae) are globose, rootless, floating aquatic plants that when abundant can completely cover the water's surface. They are tiny (0.5 to 1.5 mm long), the smallest of flowering plants (Hutchinson 1975). Several species of Lemnaceae usually occur intermixed (Fassett 1957). *Wolffia punctata* and *W. columbiana* can often be found together (Clark and Thieret 1968, Schuyler 1983; nomenclature follows Hitchcock and Cronquist 1973).

In some of the potholes near Ronan, Montana, mixed populations of *W. columbiana* and *W. punctata* are present; in others, *Wolffia* is absent. The purpose of this study was to determine whether the pattern of occurrence reflected environmental difference or chance.

Study Area

The potholes are in a cluster immediately southeast of Ninepipe Reservoir in the Mission Valley, Montana, 8 km north of St. Ignatius (Fig. 1). The potholes studied are on or adjacent to Ninepipe National Wildlife Refuge. At an elevation of 915 m, the area receives an average annual precipitation of 38 cm. The topography is a rolling and pitted morainal surface covered by dry prairies (some now plowed or mown) with pockets of wetlands and standing water.

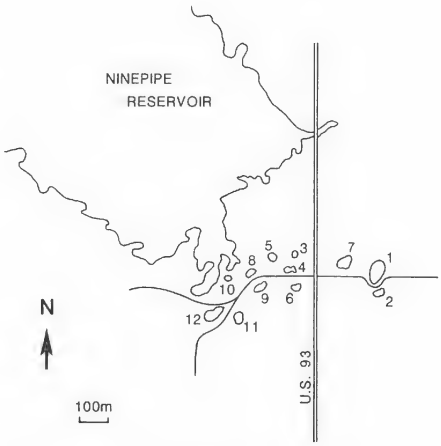

Figure 1. Locations of the twelve study potholes.

Methods

Twelve potholes were chosen for their varying amounts of *Wolffia,* close proximity to each other, and accessibility (Fig. 1). Six contained *W. columbiana* and *W. punctata* and six lacked *Wolffia.* Presence-absence of *Wolffia* was the focus of the analysis. Other Lemnaceae and common macrophytes were also noted.

The observed environmental factors were pH, conductivity, maximum depth of pothole, and

TABLE 1. Environmental characteristics (mean ± standard error, range) of potholes with and without *Wolffia*.

	Wolffia absent		*Wolffia* present	
	Mean ± s.e.	Range	Mean ± s.e.	Range
Conductivity (μmhos/cm)*	1793 ± 442	681-2825	133 ± 54	105-438
pH*	9.7 ± 0.1	9.1-10.0	9.0 ± 0.4	7.4-10.5
Maximum depth (m)*	2.0 ± 0.5	0.6-3.5	2.6 ± 0.4	1.2-3.4
Secchi disk (m)	1.1 ± 0.2	0.6-1.8	1.6 ± 0.3	0.8-2.8

*Means are significantly different at $p < 0.05$.

Secchi disk transparency. Conductivity was measured in the field at the water's surface, using a conductivity meter with thermometer. Conductivities (K) were corrected to standard temperature (25°C) using $K_c = K_{measured}/(1 + 0.0191 (T - 25))$ where T was the measured temperature. Secchi disk transparency readings were taken at midday. Maximum depth of water was obtained using a weighted rope. Water samples were collected at midday in 1 l bottles and transported to the lab in a cooler. pH was measured with a meter at 25°C.

Average conductivity, pH, depth, and transparency data were compared between potholes with and without *Wolffia* using two-tailed t-tests. Associations between *Wolffia* and other aquatic macrophytes were detected with chi-square tests on 2 x 2 contingency tables.

Results

Significant differences were found between potholes with and without *Wolffia* in three of the four physical and chemical parameters tested (Table 1). Both conductivity and pH were higher ($p < 0.001$ for both) in potholes lacking *Wolffia*. Potholes 3, 4, and 5 (Fig. 1) had the highest conductivities and had no surface water outlets. Maximum depth was lower ($p < 0.01$). Transparency was not significantly different between the two groups of potholes ($p = 0.2$).

Wolffia was positively associated with *Elodea* and *Lemna minor* ($p < 0.05$). The distribution of *Elodea* exactly matched that of *Wolffia* in these twelve potholes. *Lemna trisulca, Spirodela polyrhiza,* and *Potamogeton pectinatus* had borderline positive associations with *Wolffia;* a larger sample size is needed to resolve these borderline cases.

Discussion

Does the absence of *Wolffia* from some potholes represent a dispersal limitation or differential survival in different environments? Chance dispersal has often been implicated in explaining the spotty distribution of *Wolffia* and other Lemnaceae (Godwin 1923, Keddy 1976, Wolek 1983).

Due to their small size, whole plants could be easily transported by birds and muskrats from pothole to pothole (Jacobs 1947, Hutchinson 1975). Given the abundance of waterfowl in our study area, this short-range mobility seemed likely. However, long-distance transport of Lemnaceae by waterfowl is thought to be improbable by some because most truly aquatic plants die rapidly when dried (Jacobs 1947, Looman 1983). In our study area, potholes with no *Wolffia* were close (within 50 m) to those with abundant *Wolffia*. We suggest that these short distances between potholes are not effective barriers to its dispersal, and that environmental factors are primarily responsible for the patchy distribution of *Wolffia* in the Mission Valley.

Potholes with *Wolffia* had lower conductivities than those without it. Because the distribution of *Wolffia* was more strongly related to conductivity than pH ($t = 11.3$, $t = 5.2$, respectively), it seems likely that the absence of *Wolffia* from potholes with high conductivities reflects an intolerance to high salinity, rather than intolerance to free carbonates. For example, in pothole 10, where pH was very high (10.5) and conductivity relatively low (127 μmhos/cm), *Wolffia* was present, though rare. (Note that all Lemnaceae found in this study were present in some potholes exceeding the 8.0-8.5 pH limit reported by Hicks [1932] and Hillman [1961].)

The potholes with *Wolffia* were also deeper than those without it. Deeper potholes are more buffered against fluctuations in temperature and changes in salinity brought about by seasonal evaporation. It is possible that the shallower potholes may even lose all standing water during droughts.

Lemna minor was also absent from the three potholes with the highest conductivities, and *L. trisulca* from two of these three. These Lemnaceae also seem to be sensitive to salinity, although less so than *Wolffia*. *Lemna trisulca* at pothole 4 tolerated higher ion concentrations than *L. minor*.

Spirodela polyrhiza was present in only two potholes (8 and 11), both with relatively low conductivity and pH, but comparable to others in which it was absent. Because it is larger than the other Lemnaceae, it is perhaps less easily disseminated by birds than *Wolffia*. Therefore, *Spirodela* may be more dispersal-limited and perhaps less likely than *Wolffia* to show a tight relationship with environmental factors.

The importance of dispersal limitations to the distribution of the Lemnaceae depends on resistance to desiccation (Keddy 1976), propagule size, and the distance between patches of suitable habitat. In the Ninepipe Potholes, patches of suitable habitat are close to each other and environmental differences between potholes are related to the distribution of *Wolffia*. In this case, therefore, dispersal limitations are apparently less important than environmental limitations in controlling the distribution of *Wolffia*.

Acknowledgments

We thank Tom Golnar, Jack Stanford, and Harry Boston for advice; John Madsen, Patricia Muir, and anonymous reviewers for comments on the manuscript.

Literature Cited

Clark, H. L., and J. W. Thieret. 1968. The duckweeds of Minnesota. Mich. Bot. 7:67-76.

Fassett, N. C. 1957. A Manual of Aquatic Plants. University of Wisconsin Press, Madison.

Godwin, H. 1923. Dispersal of pond floras. J. Ecol. 11:160-164.

Hicks, L. E. 1932. Ranges of pH tolerance of the Lemnaceae. Ohio J. Sci. 32:237-241.

Hillman, W. S. 1961. The Lemnaceae, or duckweeds. Bot. Rev. 27:221-287.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle.

Hutchinson, G. E. 1975. A Treatise on Limnology, Vol. III. Wiley and Sons, New York.

Jacobs, D. L. 1947. An ecological life history of *Spirodela polyrhiza* (greater duckweed) with emphasis on the turion phase. Ecol. Monogr. 17:437-467.

Keddy, P. A. 1976. Lakes as islands: the distributional ecology of two aquatic plants, *Lemna minor* L. and *L. trisulca* L. Ecology 57:353-359.

Looman, J. 1983. Water meal, *Wolffia arrhiza* (Lemnaceae) in Saskatchewan. Can. Field-Naturalist 97:220-222.

Schuyler, A. E. 1983. Distributional notes on northwestern Montana aquatic vascular plants—1982. Bartonia 49:52-54.

Wolek, J. 1983. Determinants of community structure for the pleustonic plants (the Lemnetea class). Ekologia Polska 31:173-200.

Received 2 April 1986
Accepted for publication 8 July 1986

Russell N. Holmes, Bureau of Land Management
777 N.W. Garden Valley Blvd., Roseburg, Oregon 97470

Population Monitoring of *Phacelia verna:* A Federal Candidate Species

Abstract

Population monitoring of *Phacelia verna* (Umpqua phacelia) was conducted over a five-year period between 1981 and 1985 to determine the effects of adjacent logging and road construction. Six plots were randomly selected along two transects in a single population. Counts of the number of individuals of *P. verna* in each plot were made twice during each growing season. Counts of other vascular plant species were made once during each growing season. Density (indiv/m^2) of *P. verna* was found to vary significantly between plots but rarely between years. Similar results were found among associated species. Large fluctuations in seedling survival and capsule production were observed in *P. verna* throughout the study. These fluctuations did not correlate well with adjacent logging activity and are most likely explained by fluctuations in environmental parameters.

Introduction

Phacelia verna is a small annual in the Hydrophyllaceae (Waterleaf Family). White to light blue flowers are produced on a scorpioid cyme between April and June. Stems are up to 2.5 dm high, single or branched, and coarsely hairy. Leaves are alternate. More detailed descriptions can be found in Howell (1895), Abrams (1951), and Peck (1961).

Habitat requirements appear to be quite specific. All reported sightings have been on grass- and moss-covered balds or rock outcrops (Howell 1953; Oregon Natural Heritage Data Base unpublished data). Elevations of known sites range from 152 to 2011 m. Slopes are moderate, ranging up to 95% and the aspect usually is southerly from west to east. Balds where *P. verna* is found are wet in the spring when seeds germinate but begin to dry rapidly by the time of anthesis. The habitat becomes extremely dry and hot when capsules dehisce and begin disseminating seeds in late June or early July.

Distribution is restricted primarily to the Umpqua River drainage of Douglas and Coos Counties where a total of 63 sites are known. Sites are at times highly aggregated with as many as eight occurring in a single section. Two sites are known outside the Umpqua Valley, one just north of the Calapooya Divide in Lane County and another near King Mountain in Josephine County.

Phacelia verna is presently under review as a Candidate Species by the U.S. Fish and Wildlife Service (1985). The fact that there are relatively few populations, each having a limited distribution, combined with threats posed by intensive forest management practices, indicate it is biologically appropriate for *P. verna* to be listed as threatened or endangered under the Endangered Species Act. Further field searches and an evaluation of the plants' susceptibility to threats must be made before a final decision can be reached. The purpose of this study was to evaluate the response of *P. verna* to adjacent logging activity and road construction, and to determine if protection measures implemented in the Timber Sale Plan were adequate. These measures included:

(1) keeping yarder lines at least 200 feet and roads at least 100 feet away from the population;
(2) rocking road surface to help control dust during loading and hauling operations;
(3) prohibiting grass mulching of the road cut within 300 feet of the *P. verna* habitat;
(4) prohibiting slash burning between 1 March and 15 July to insure seed set if the fire should escape; and
(5) prohibiting herbicide application within 250 feet of the *P. verna* habitat.

Study Area

The study area is a typical sparsely vegetated bald located on the west slope of the Cascades in Douglas County (Sec. 27 NE1/4SW1/4, T. 25 S., R. 1 W., W.M.). The bald covers approximately 0.1 ha along the crest and upper slope of Williams Ridge at 975 m. Aspect of the bald is west with a 40-45 percent slope. The surrounding forest is a mixed conifer community consisting of *Pseudotsuga menziesii, Tsuga heterophylla,* and *Libocedrus decurrens* typical of the *Tsuga*

heterophylla zone as described by Franklin and Dyrness (1973). Most of the precipitation occurs in the winter months, with an average of 87% occurring October through April (McNabb *et al.* 1982, Froehlich *et al.* 1982). Snow can occur and accumulate between November and April. A thin soil over volcanic rock supports a community of moss, annuals, and scattered perennials. *Mimulus alsinoides, Collinsia parviflora, Trifolium variegatum, Gilia capitata,* and *Polygonum spergulariaeforme* are among the more frequently encountered annuals. The more common perennials include *Eriogonum compositum, Lomatium hallii,* and *Lupinus albifrons.*

Methods

Methods of monitoring were developed through consultation with the U.S. Fish and Wildlife Service (1980). Two transects were established across the bald with a total of six one m^2 plots randomly selected along the two transects. Population counts were made twice a year; once at the time of seedling establishment (22-27 April) and once at the time of peak flowering (13 May-1 June). A vegetation analysis was made at the time of peak flowering by identifying all species occurring in the six one m^2 plots and counting the number of individuals for each species. Litter accumulation was estimated at this time by determining the depth to bedrock using a metal spike graduated in centimeters that was permanently placed in each plot. Several photographs were taken at the time of peak flowering to document visually the condition of the habitat each season. The average number of capsules per plant for *P. verna* was estimated by counting capsules on 10% of the individuals in each plot once the plants reached fruit maturity (28 June-1 July). Plant identifications were made using Hitchcock and Cronquist (1973) and Peck (1961). Temperature was recorded using a model 5022 Weathertronics Hi Q hygrothermograph. Data was organized according to a crop year (October through September).

Results

Precipitation was recorded each month throughout the study at the National Forest Service Steamboat Ranger Station 5.8 km southeast of the study site by the Douglas County Water Resources Survey (Table 1). Monthly precipitation ranged from 0 cm in August 1981 to 49.4 cm in December 1981. Total annual precipitation was lowest in crop year (CY) 1981 with 112.9 cm recorded. Only minor differences in annual precipitation were observed during the next three year period, ranging from 168.3 cm to 172.4 cm. A total of 140.2 cm of precipitation was recorded in CY 1985. Spring precipitation was lowest in CY 1982. Precipitation between April and June of that year was 20.5 cm, 12.2% of the annual amount. May was exceptionally dry with only 0.7 cm of precipitation. In comparison, at least 3.7 cm occurred in any single month during this period in the other three years of the study. Spring precipitation was highest during the spring of 1984. Precipitation between April and June was 43.7 cm which was 25.4% of the annual amount, over twice the amount observed in CY 1982.

TABLE 1. Monthly precipitation for CY 1981-1985.

	Precipitation (cm)				
Month	1980-1	1981-2	1982-3	1983-4	1984-5
Oct	7.8	12.6	17.6	5.6	19.0
Nov	10.8	21.1	15.0	31.6	43.5
Dec	23.1	49.4	33.6	37.8	17.4
Jan	5.6	17.4	13.9	7.1	1.6
Feb	18.0	16.5	30.3	24.3	13.9
Mar	11.2	16.0	24.1	18.4	14.9
Apr	8.6	14.5	12.1	20.0	8.5
May	11.0	0.7	7.2	12.5	4.3
June	7.9	5.3	3.7	11.2	8.8
July	1.4	1.9	8.2	0.8	0.6
Aug	0.0	1.4	5.3	0.7	1.1
Sept	7.5	11.5	1.4	2.1	6.6
Total	112.9	168.3	172.4	172.1	140.2

Temperature measurements were recorded during the last three years of the study (Table 2). Mean low temperatures were less than 1° C between November and March for all years. Mean high temperatures did not exceed 15.4° C for the same period and monthly mean temperatures did not exceed 7.3° C. Mean temperatures progressively increased to a high in August 1983 and in July of 1984 and 1985 ranging from 17.1° C to 21.1° C. Extreme low temperatures occurred in December of CY 1983 and 1984 and in February of CY 1985. Temperatures fell to −7°, −18°, and −13° for these

TABLE 2. Monthly temperatures (°C) for CY 1983-1985.

Month	Mean High			Mean Low			Monthly Mean		
	1982-3	1983-4	1984-5	1982-3	1983-4	1984-5	1982-3	1983-4	1984-5
Oct	16.2	17.4	11.3	4.6	5.0	1.6	10.4	11.2	6.4
Nov	6.8	4.2	4.5	−1.4	−0.6	−1.0	2.7	1.8	1.8
Dec	4.5	1.0	5.1	−2.0	−3.7	−4.0	1.3	−1.4	0.6
Jan	*	10.3	15.4	*	−1.0	−0.9	*	4.7	7.3
Feb	*	7.6	5.6	*	−1.5	−3.4	*	3.1	1.1
Mar	7.4	10.2	6.6	0.4	0.7	−3.1	3.9	5.5	1.8
Apr	12.3	8.9	14.5	−0.5	−1.6	1.8	5.9	3.7	8.1
May	17.9	14.8	16.3	4.7	2.0	2.3	11.3	8.4	9.3
June	19.2	18.1	23.2	5.7	4.7	7.4	12.4	11.4	15.3
July	20.2	27.2	30.0	7.5	9.9	12.2	13.9	18.6	21.1
Aug	23.7	26.3	26.2	10.6	9.0	9.1	17.1	17.7	17.7
Sept	21.8	23.4	19.4	6.9	6.7	5.7	14.4	15.0	12.6

*Recording instrument removed because of deep snow and adverse weather conditions.

three consecutive years. Freezing or below temperatures occurred through May 15, 1983, June 10, 1984, and June 24, 1985. Extreme high temperatures occurred on May 28, 1983 (39° C), July 15, 1984 (35° C), and June 17, 1985 (37° C).

Numbers of *P. verna* varied significantly throughout the study. Average plot densities dropped from 66.0 individuals per m^2 in CY 1981 to 1.8 in CY 1982 (Figure 1). The population rebounded in CY 1983 to 68.0 individuals per m^2 and then fell again to near 1982 levels in CY 1984 and CY 1985. Comparisons of mean plot densities using a two tailed t test revealed that mean plot density was significantly less in CY 1982 as compared to CY 1981 and CY 1983 but was statistically equivalent to CY 1984 and CY 1985 ($p = 0.05$). Variation between plots was high all five years.

Similar results were observed among associated species (Table 3). Species fluctuated widely between years but variation between plots was high enough that these fluctuations were rarely significant. Several annuals (*Lotus micranthus, Mimulus alsinoides,* and *Montia perfoliata*) and one biennial (*Erysimum asperum*) were not observed in any plots during CY 1982 but were observed in all other years. One perennial, (*Castilleja pruinosa*) observed in CY 1981 was not observed in subsequent years. The only significant variation occurred between CY 1981 and CY 1982 for *Collinsia parviflora,* between CY 1982 and CY 1984 for *Montia perfoliata* and between CY 1982 and CY 1985 for *Polygonum spergulariaeforme.* In all cases, CY 1982 was significantly less ($p = 0.05$).

Very little variation was observed in other measured components. Percent non-vascular cover remained essentially unchanged (Table 4). Changes in litter accumulation were negligible.

Large fluctuations in seedling survival and capsule production were observed throughout the study. Mortality was 84% in CY 1982 (Table 5). Mortality dropped to zero or near zero in the last three years of the study. Capsule production decreased from 8.4 per plant in CY 1981 to 4.9 in CY 1982 and 3.9 in CY 1983. A sharp rise to 7.2 in CY 1984 and 6.0 in CY 1985 returned capsule production to near 1981 levels.

Discussion

Results have shown that density of vascular plant components of the bald community fluctuate substantially between plots but rarely between years. Only three out of sixteen associated species (*Montia perfoliata, Polygonum spergulariaeforme,* and *Collinsia parviflora*) showed any significant variation between years and in each case 1982 was lower than all other years. Similarly population levels of *P. verna* were lower in 1982 as compared to 1981 and 1983.

These fluctuations have not correlated very well with logging activity. Road construction began in November 1982 and continued intermittently throughout the following winter and

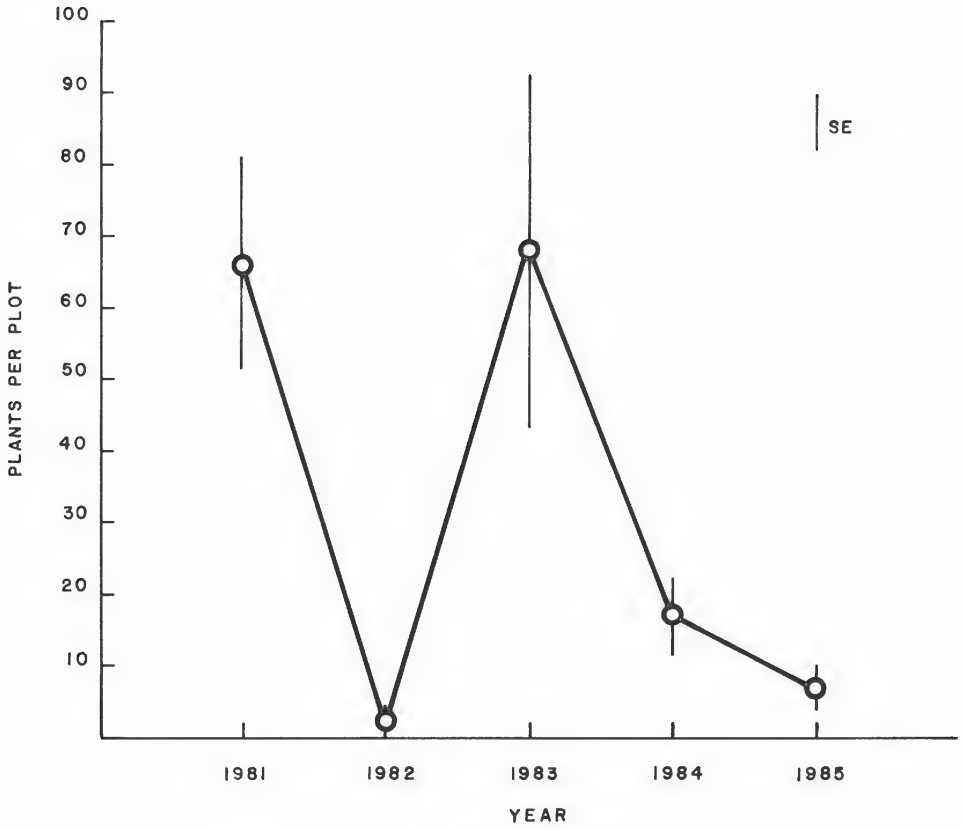

Figure 1. Mean plot densities of *Phacelia verna* 1981-1985

spring. Logging on one of two adjacent units began in August and was completed in November 1983. The second unit was logged between May and September 1984. Some of the most intensive logging adjacent to the study area occurred immediately prior to and during the growing season that produced the greatest number of *P. verna* which was significantly more than the previous year when no logging occurred. These observations seem to indicate that the protection measures implemented in the timber sale plan were effective. This is further supported by photos of the habitat which show no disturbance or visible change of any sort over the course of the study. Delayed impact however, is possible. Monitoring will have to be continued to determine if the relatively low population levels observed in 1984 and 1985 persist.

Fluctuations in community structure are most likely explained by fluctuations in environmental parameters, in particular, precipitation and temperature. This would seem to explain the low population levels of *P. verna* in 1982. A cold late spring with snow remaining on the ground well into April (field notes) followed by unusually dry conditions in May (Table 1) very likely contributed to the low germination and high mortality observed that year (Table 5). The rebound of *P. verna* in 1983 provides evidence of substantial seed storage in the soil.

TABLE 3. Average plot densities (indiv/plot) at time of peak flowering 1981-1985.

Species	Plot Density				
	1981	1982	1983	1984	1985
Arenaria stricta	0.0	0.3	0.0	6.0	0.5
Berberis nervosa	0.2	0.2	0.2	0.2	0.3
Castilleja pruinosa	0.2	0.0	0.0	0.0	0.0
Collinsia parviflora	15.2	0.7	34.7	64.8	13.7
Epilobium minutum	41.2	4.5	5.0	23.3	3.7
Eriogonum compositum	7.7	11.5	14.0	11.8	13.7
Erysimum asperum	0.8	0.0	0.3	0.2	0.2
Gilia capitata	19.8	0.5	16.7	4.7	7.7
Lomatium hallii	6.2	5.2	3.0	19.2	10.5
Lotus micranthus	7.0	0.0	2.0	1.2	0.7
Lupinus albifrons	1.8	0.3	0.2	0.3	0.3
Microsteris gracilis	35.5	0.8	10.8	12.7	6.7
Mimulus alsinoides	5.3	0.0	4.8	14.2	8.3
Montia perfoliata	32.0	0.0	10.5	23.5	2.5
Phacelia verna	66.0	1.8	68.0	17.0	7.3
Polygonum spergulariaeforme	28.2	1.3	14.3	23.5	23.8
Trifolium variegatum	5.8	3.3	6.0	2.5	7.0

TABLE 4. Vegetation analysis at time of peak flowering 1981-1985.

Component	Component Value				
	1981	1982	1983	1984	1985
% Grass Cover	3.2	1.0	1.3	1.5	1.3
% Non Vascular Cover	86.0	86.0	85.5	90.5	93.8
Litter Accumulation (cm)	3.9	3.6	4.0	4.8	4.4

TABLE 5. *Phacelia verna* seedling mortality 1981-1985.

Year	Ave. Number per plot		Mortality	
	Seedling	Peak Flowering	Individuals	Percent
1981	—	66.0	—	—
1982	11.5	1.8	9.7	84
1983	69.8	68.0	1.8	3
1984	17.0	17.0	0.0	0
1985	7.5	7.3	0.2	3

Dependency of *P. verna* on precipitation alone is not supported by the data collected to date. Regression of *P. verna* density against precipitation for the months of April through June, April through May, and May alone and against percent of annual precipitation for the month of May did not show any significant relationship for all years of the study ($p = 0.05$).

Further research and monitoring needs to be conducted before the ecology of *P. verna* can be clearly understood. In particular, the response of *P. verna* to fluctuations in environmental parameters needs to be more thoroughly examined. Data on seed viability, germination requirements, and in situ substrate seed densities needs to be obtained.

Acknowledgements

Appreciation is extended to Miles Dwan and Gary Burson, temporary botanists for the Bureau of Land Management, for their assistance in establishing transects and collecting data, to the U.S. Fish and Wildlife Service for their technical support, and to Drs. Kenton Chambers and David Wagner for critical review of this manuscript.

Literature Cited

Abrams, L., and R. S. Ferris. 1951. Illustrated flora of the Pacific States. Vol. 3. Stanford University Press, Stanford.

Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA For. Ser. General Tech. Rep. PNW-8, Pac. Northw. For. Range Exp. Sta., Portland, Oregon.

Froehlich, H. A., D. H. McNabb, and F. Gaweda. 1982. Average annual precipitation in southwest Oregon, 1960-1980. Oregon State University Ext. Ser. Misc. Publ. 8220, Corvallis, Oregon.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle.

Howell, J. T. 1953. Some places where Phacelias grow. Leafl. West. Bot. 7:11-15.

Howell, T. 1895. New species of Pacific Northwest plants. Erythea 3:35-36.

McNabb, D. H., H. A. Froehlich, and F. Gaweda. 1982. Average dry-season precipitation in southwest Oregon, May through September. Oregon State University Ext. Ser. Misc. Publ. 8226, Corvallis, Oregon.

Peck, M. E. 1961. A manual of the higher plants of Oregon. Second Edition. Binfords & Mort Publ., Portland.

U.S. Fish and Wildlife Service. 1985. Endangered and threatened wildlife and plants; Review of plant taxa for listing as endangered or threatened species; Notice of review. Federal Register 50(188):39526-39584.

_____. 1980. Informal consultation re: Impact of Williams Ridge logging project on *Phacelia verna*. Memorandum Correspondence, November 13, 1980, U.S. Fish and Wildlife Service Area Office, Olympia, Washington.

Received 3 March 1986
Accepted for publication 9 July 1986

Ronald B. Newton and **Kerry P. Reese**
College of Forestry, Wildlife and Range Sciences
University of Idaho, Moscow, Idaho 83843

and

Wayne E. Melquist, Idaho Department of Fish and Game
P.O. Box 25, Boise, Idaho 83707

Northern Idaho Citizens Survey on Nongame Wildlife and Idaho Income Tax Checkoff Program

Abstract

A mail survey was conducted of 300 randomly selected residents of northern Idaho to obtain their attitudes toward nongame animals and the Idaho Income Tax Checkoff Program. Birds were most interesting to residents compared to mammals, fish, and reptiles. Most people were unaware of the majority of current nongame projects funded by the Idaho Department of Fish and Game. In addition, the public does not appear well informed about nongame wildlife or about the support required to help sustain their populations. Only 50% of respondents knew about the tax checkoff program. Approximately two-thirds of the respondents that used tax consultants were not informed by the consultants of the tax checkoff program. To increase donations to nongame through the tax checkoff program the following recommendations are made: 1) a more effective publicity campaign to inform the public of the value of nongame is needed, 2) contributors should know how their donations will be used, 3) a large percentage of nongame projects should appeal to the public's interest, and 4) increased cooperation from tax consultants is necessary.

Introduction

Funding nongame projects has been a continual problem for state wildlife agencies. A variety of approaches have been tried including voluntary contributions, sale of decals and stamps, general appropriations, state sales tax, personalized license plates and income tax checkoffs. Income tax checkoffs have become the most significant source of revenue. Since 1978, thirty-one states have initiated checkoff programs whereby taxpayers can contribute a portion of their tax refund to nongame programs. In 1984, taxpayers across the country donated $9 million to nongame (McCance 1985).

While apparently a successful source of funds, the tax checkoff program may not be a stable long-term revenue source. Harpman and Reuler (1985) demonstrated a declining trend in revenue generated in most states using the tax checkoff approach. As other competing checkoffs, such as Child Abuse and Olympics, are added to a state's tax form, decreased contributions to nongame are likely to follow (Applegate and Trout 1984).

Idaho's nongame program began in the 1981 tax year with contributions of $106,000 through the income tax checkoff. Keller (1984) indicated that approximately 6% of Idaho taxpayers contributed $106,200 for the 1982 tax year. Since then, contributions have declined yearly until in 1984 only $80,000 was received. Checkoffs for Child Abuse and Drug Enforcement are presently competing with nongame for voluntary contributions from taxpayers.

To maximize revenue derived from the income Tax Checkoff Program, general information is needed about the public's attitude and behavior toward the tax checkoff program and nongame wildlife. Our objectives were to determine the public's level of awareness concerning the Idaho Department of Fish and Game Nongame Program, to determine characteristics of contributors to the nongame fund and to determine public attitudes toward nongame and the tax checkoff program. To obtain this information we conducted a survey of the residents in northern Idaho.

Methods

A random sample of 300 of a population of 95,000 names was surveyed by mail in the spring of 1985 using the procedures outlined in Dillman (1981). The area covered was from Lewiston north to the Canadian border. The survey contained 33 questions concerning the citizens' knowledge of nongame animals, current nongame projects

and the income tax checkoff program. The survey, with an introductory letter, was mailed on 22 March 1985 with a self-addressed, stamped envelope enclosed. After 2 weeks, a postcard was sent in an attempt to encourage participation. After 2 more weeks another survey was mailed as a reminder to participants misplacing or losing their surveys and to further encourage participation.

Results

One hundred seventy-four (58%) surveys were returned. All major areas were represented. The first mailing yielded 135 returns, the follow-up mailing resulted in a return of 39 surveys which indicated a follow-up was important. Age ranged from 21 to 85 years old. Education ranged from 8 to 22 years.

Fifty-three percent of respondents knew that the Idaho Department of Fish and Game is currently involved in at least one nongame project (Table 1). Familiarity was the highest among the more educated and those in age group 20-29, 30-39 and 60-69 years.

Contributors to the Tax Checkoff Program

Respondents contributing to the 1981, 1982, and 1983 Nongame Income Tax Checkoff Program comprised 6%, 11%, and 12%, respectively. Although Keller (1984) indicated that 6% of Idaho taxpayers donated in 1982, our data cannot be discounted because information on donations of southern Idaho taxpayers is unknown. Of the total respondents asked about the 1984 Income Tax Checkoff Program, 23% indicated they intended to or had contributed. Verification of contributions cannot be made, therefore the validity of these results is unknown.

Age was a factor among contributors with more donations coming from those in age groups 30-39 and 40-49 years. Sixty percent of all donations were received from these age groups compared to 21% from the 50-59 and 60-69 age groups and 18% from the 20-29 age group. Education was also related to participation in the Tax Checkoff Program. Twice as many participants with at least some college (58%) compared to high school graduates (30%) and over 5 times more than those with less than 12 years education (11%) said they had or intended to participate in the 1984 program.

TABLE 1. Percentage of the 174 respondents that knew about nongame projects and the percentage of respondents that favor these programs.

Project	% know of	% in favor
Raptor nesting platforms	29	39
Woodland caribou research	28	39
Bluebird nest boxes	25	39
Peregrine falcon reintroduction	19	33
Nongame video programming on PBS	17	40
Fish hatchery/waterbird literature search and assessment in Idaho	16	33
Raptor rehabilitation	12	23
Landscaping for wildlife	10	22
Ecological study of colonial-nesting waterbirds in eastern Idaho	10	17
Nongame wildlife data collection	9	22
Boreal owl research	9	18
Educational resource center for Project WILD	9	16
Urban wildlife	8	18
Idaho ground squirrel	8	12
Nongame species ecological leaflets	3	14
Translocation of Shoshone sculpin	3	9

Of the 165 respondents that either hunt or fish, 22% said they had or intended to contribute to the 1984 program. Urbanites and rural dwellers were equally likely (23%) to have contributed or intended to contribute to the 1984 program.

The U.S. Olympic Fund and the Drug Enforcement Fund appeared to have little impact on the amount contributed to the Nongame Tax Checkoff Fund. Of respondents contributing to the 1983 Nongame Program, 90% said they would not have given more if the U.S. Olympic or the Drug Enforcement Funds were not on the list. Only 7% contributed to the above two funds. Eighty-two percent would not be inclined to donate more if they were somehow recognized for their donation. However, twenty-four percent said they would be more inclined to donate to the program if they were given an opportunity to suggest a specific nongame management project for possible funding.

Budget Expenditures

A series of questions were asked regarding expenditure of monies for various nongame subjects. Birds and endangered species were most popular with respondents (Table 2).

Respondents who had knowledge of the Idaho Nongame Income Tax Checkoff Program (50%)

TABLE 2. Respondents' recommendation as to how budget should be managed for nongame animals.

Subject	% of Budget
a. Birds	58
Fishes	22
Mammals	12
Reptiles	8
b. Threatened or endangered species	42
Species that cause damage or disease	26
Species the public can observe	20
Species on which research may lead to greater scientific knowledge	12
c. Increase population size and distribution	30
Work on lands to improve habitat	26
Caring for sick or injured nongame wildlife	16
Determine numbers and distribution of nongame wildlife	16
Acquire land for nongame wildlife	12

were asked to identify the origin of their information (Table 3). Of those naming a source for their knowledge of the program, 34% said they had or intended to contribute to the 1984 program.

Of the 92 respondents that had professional tax consultants prepare their taxes, 67% were not informed by their consultant of the Idaho Nongame Tax Checkoff Program. Those that were informed of the program (30%) stated they were not given any advice about contributing. A few (2%) were advised not to contribute. Of the 40 respondents that reported preparing their own taxes, 22% contributed or intended to contribute.

Other Pertinent Information

Participants were asked to indicate the types of outdoor and nature activities in which they participate. Eighty percent fish, 76% camp, 62% picnic, 58% view wildlife, 58% hunt, 53% hike, 32% photograph nature, 18% birdwatch, 14% engage in nature study, and 3% trap. They were also asked if they had a particular animal that they think should be considered for a nongame project. Nineteen respondents named six game animals: pheasant *Phasianus colchicus,* black bear *Ursus americanus,* cougar *Felis concolor,* elk *Cervus elaphus,* rabbit *Sylvilagus nuttallii* and northern pike *Esox lucius;* seven nongame: caribou *Rangifer tatandus,* mountain bluebird *Sialia currucoides,* red squirrel *Tamiasciurus hudsonicus,* Peregrine falcon *Falco peregrinus,* barred owl *Strix varia,* bald eagle *Haliaeetus leucocephalus,* and wolf *Canis lupis* and two fur bearers. Obviously the public does not readily distinguish game from nongame species.

TABLE 3. Respondents' sources of information about the nongame tax checkoff program.

Source	% (N = 174)
Tax form	28
Television	23
Idaho Wildlife magazine	16
Local newspaper	12
Radio	8
Tax consultant	7
Friend or associate	6

Sixty-one percent believed that their donations to the Nongame Program would aid mammals, birds, reptiles and amphibians that would be otherwise ignored. Fifty-three percent believed it would result in improved habitat conditions for nongame species. Fifty percent assumed that donating would lead to a higher quality environment in Idaho, while only 9% felt that donating would have no effect on nongame wildlife. Nearly 30% believed donating would lead to more recreational opportunities to view nongame wildlife. The monetary aspect of donating apparently is of little concern, for only 15% stated that donating would leave them with less money to buy things more important to them.

Last of all, 33% believed that donating would lead to more bureaucracy. Of the more educated respondents, 1 out of every 4 believed this to be true. The different age groups varied in their response, with the 30-39 age group lowest with 14% believing more bureaucracy would be created while the highest was the 60-69 age group with 32% believing this would occur. However, we do not know if these individuals did not contribute because of this belief.

Participants were given an opportunity to offer their ideas on how to increase revenue for nongame. Some interesting and creative ideas were rendered by 50 (32%) participants. Some general recommendations were: raffles, lotteries, adopt an animal project by school children, walkathons, a general tax for wildlife, assistance from private organizations, fines for people

damaging wildlife habitat, and donation of recyclables. An Idaho recreation fee was recommended similar to the one used in Montana. Those individuals such as campers, hikers, motorcyclists, and fourwheelers would pay an established fee for use of state and federal land. Increasing fees for hunting and fishing licenses and using a portion of this revenue for nongame was recommended by 24% of those submitting ideas.

The most frequently recommended idea (40%) was to obtain the public's interest by educating them to the benefits of nongame animals. As one participant stated, "Let the public get involved in the planning of nongame projects within their community. Use public television to spread the word. Show the public that donated money is not being wasted. Better education of the people should lead to better understanding which will hopefully lead to greater contributions."

Discussion

Northern Idahoans are avid outdoors-people. Nongame wildlife is a part of their outdoors and a concern for it is clearly shown in this study. However, concern does not alleviate the perplexity of supporting nongame wildlife. In 1982, Idaho had only 6% of the taxpayers contributing to support nongame wildlife (Keller 1984). While this was slightly above the national average in percent donating, the average dollar amount contributed ($4.43) was below average (Keller 1984). Therefore, the important challenges are getting a greater percentage of the taxpayers to participate and increasing the amount donated from contributors.

Public education regarding the importance of nongame wildlife is integral. Achieving such awareness will involve a considerable financial investment. But with greater public awareness it should be easier to convince people to support nongame wildlife. In addition, the public must be informed of current projects involving nongame. Although half of the respondents knew the Idaho Department of Fish and Game was involved in various nongame projects, the highest report of knowledge of a nongame project was 29% (establishment of nesting platforms for raptors). Only 3% had knowledge of the translocation of Shoshone sculpin *Cottus greenei,* a rare *fish, and nongame species ecological leaflets.* Unfamiliarity about the sculpin project might be expected because of the regional nature of this survey, but nongame leaflets have been published in the Idaho Wildlife magazine and are available at all regional offices.

Nongame projects should be geared to the public's interest. However, species less attractive to the public should not be neglected. A program with a number of projects established from public input could be implemented. One of the most favored projects was nongame video programming on the Idaho Education/Public Broadcasting System. This could be a message saying the public is eager to learn about nongame wildlife.

Contrary to Applegate's (1984) New Jersey survey, television was the second most effective way of reaching the public. This could be associated with the remoteness of northern Idaho. The Tax Checkoff Program is seasonal, so money spent on television ads should be concentrated just prior to and during income tax time in an effort to keep expenditures to a minimum. In a further study, Applegate and Trout (1984) concluded that promotional efforts on both radio and television appear to increase checkoff revenue. Radio appears to be the most effective followed closely by television. As stated in their report, "the regression model suggests that promotional dollars invested in radio are returned twenty-fold in checkoff revenue." Although radio appeared insignificant in this survey, it still might be an effective means of public information when considering the entire state. Additional special interest programs are likely to be added to the tax form, increasing competition for checkoff dollars as has occurred in other states (Applegate and Trout 1984). While our results did not support this, we believe it likely to occur in the future. The loss in revenue could be significant, so an increased publicity effort will probably be needed to at least maintain current revenue level.

Idaho does not specify the final destination of its tax checkoff dollars within the Nongame Fund. This could be detrimental to potential revenue according to Applegate and Trout (1984). A substantial increase in revenue was obtained by those states that specified where the donation was destined compared to those with a general purpose (Applegate and Trout 1984). Although this is a tentative conclusion, it appears that an increase in participants can be obtained if they know what their contribution will support. This

could be a way of satisfying the 33% of northern Idaho residents that their donation will not contribute to more bureaucracy and induce them to participate in the Tax Checkoff Program.

A means to enhance donations from citizens using tax consultants needs to be developed. A majority of the respondents used a consultant to prepare their 1984 income taxes. Most of these were not informed of the Income Tax Checkoff Program. New Jersey has experienced a similar problem (Applegate 1984). There could be a substantial increase in revenue if tax consultants would inform clients of the Tax Checkoff Program.

The Income Tax Checkoff Program has been a key source of financial support to current nongame wildlife projects. However, its dependability is questioned. The success of the program has enticed a flooding of tax forms with other checkoffs. As each additional checkoff is added to the tax form, a larger decrease in revenue is likely to follow. Harpman and Reuler (1985) demonstrated a downward trend in revenue by most states using the Income Tax Checkoff Programs, indicating that this funding avenue does not appear to have long-term stability. If the addition of other checkoffs remains unrestrained, a significant decrease in contributions may occur.

In 1982 almost the entire amount of contributions in Idaho was received from those individuals making $60,000 or less (Harpman and Reuler 1985). Fifty percent of the contributions were donated by people with an income of $30,000 or less. Donations did increase with income, but not proportionally. From this analysis, Harpman and Reuler concluded that the checkoff is regressive and lower income taxpayers pay more than their "fair share" of the cost of supporting nongame.

Recommendations

1. To gain voluntary contributions from taxpayers an effective publicity campaign must be waged. Competition for the dollar is increasing by the addition of more checkoff programs to the tax form. The public must be convinced that the state's wildlife is an important ecological component that relies on contributions from the state's citizens. Henderson (1984) described an elaborate and effective publicity campaign implemented by the state of Minnesota.
2. Specific designation of checkoff dollars is recommended. We should eliminate the doubt as to where contributions are being funneled.
3. Species and projects of public interest should be obtained so projects can be programmed to these interests, giving the public a feeling of participation.
4. Finally, an effort to gain support from tax consultants has to be implemented. It is apparent that tax preparers in northern Idaho are not informing their clients of the Income Tax Checkoff Program which eliminates a large number of potential contributors.

The ability of the Income Tax Checkoff Program as a reliable source of income is in doubt. Current studies show a decline in income from a majority of the states using checkoff programs. Although the checkoff cannot be considered an ideal fund raising mechanism (Harpman and Reuler 1985), it must not be abandoned until a more equitable and reliable system can be found.

Acknowledgements

We wish to thank the Idaho Cooperative Fish and Wildlife Research Unit for support, D. F. Newton for her assistance in several phases of the work, and all respondents for their cooperation.

Literature Cited

Applegate, J. E. 1984. Nongame tax checkoff programs: A survey of New Jersey residents following the first year of contributions. Wildl. Soc. Bull. 12:122-128.

Applegate, J. E., and J. R. Trout. 1984. Factors related to revenue yield in state tax checkoffs. Trans. N. Amer. Wildl. Nat. Resour. Conf. 49:199-204.

Dillman, D. A. 1981. Mail and telephone surveys: The total design method. Wiley and Sons, New York.

Harpman, D. A., and C. F. Reuler. 1985. Economic aspects of the nongame checkoff. Nongame Newsletter 3:4-8.

Henderson, C. L. 1984. Publicity strategies and techniques for Minnesota's nongame wildlife checkoff. Letter Minnesota Dept. Natur. Resour. St. Paul, Minnesota.

Keller, B. 1984. Nongame notes. Idaho Wildl. News Jul/Aug.

McCance, B. 1985. Nongame checkoffs raise $9 million in 1984. Nongame Newsletter 3:1-3.

Received 21 April 1986
Accepted for publication 1 September 1986

Jeffrey C. Mosley and **David B. Wester**
Department of Range and Wildlife Management
Texas Tech University, Lubbock, Texas 79409

and

Stephen C. Bunting, Department of Range Resources
University of Idaho, Moscow, Idaho 83843

Estimating Herbaceous Yield from Species Frequency

Abstract

Frequency sampling is a useful method for quantitatively classifying and monitoring vegetation composition. However, it does not provide herbage production data needed to calculate and monitor carrying capacity. Frequency-yield relationships were examined on 12 dry mountain meadow sites in central Idaho. Herbaceous yield and species frequency were sampled, and regression equations were developed to relate these two parameters. Significant regressions ($P < 0.10$) were achieved for 21 of 30 species with most r^2 values 0.70 or greater. Estimated total site yields were calculated from individual species' regressions. Estimated total yields and actual total yields did not differ ($P > 0.05$). Development of similar area-specific regression equations may enable land managers to obtain satisfactory yield estimates from frequency data. This may enable land managers to use the same sampling method for monitoring species composition and calculating carrying capacity from year to year.

Introduction

Herbaceous yield is a vegetation attribute widely-used to quantitatively estimate species composition. However, composition estimates based on yield depend on when sites are sampled because of seasonal (Odum 1960) and yearly (Craddock and Forsling 1938, Harris 1954) climatic fluctuations. Therefore, the true effect of management practices is often masked by changes in weather. For these reasons frequency data have been proposed as an alternative means to monitor changes in species composition (USDA 1981).

Perennial plant frequency does not significantly fluctuate annually or seasonally since it is partially determined by density (Hyder *et al.* 1966). Frequency sampling is also more repeatable between observers because its measurement is less subject to personal bias. This reliability is attractive to land management agencies whose data are usually collected by an ever-changing field staff. However, a common criticism of frequency sampling is that it does not provide herbage production data needed to calculate and monitor carrying capacity. Species composition can be classified and monitored using frequency data (Smith 1982, Mosley *et al.* 1986), but presently land managers are unable to estimate a species' or site's yield from species frequency. This study was initiated to examine whether satisfactory yield estimates could be obtained from frequency data.

Study Area and Methods

Dry mountain meadows of central Idaho were selected as the vegetation type in which to test the hypothesis that herbaceous yield could be estimated from species frequency. Study sites were located on the Lowman Ranger District of the Boise National Forest, approximately 200 km northeast of Boise, Idaho. Meadows in this region provide most of the summer forage for domestic livestock grazing mountain rangeland; the grazing season typically extends from 1 July to 15 October. Study sites range in elevation from 1950 to 2045 m. According to U.S. Forest Service (USFS) records, annual precipitation on these sites varies from 510 to 1020 mm with approximately 70 percent occurring as snow. Precipitation was considered normal during the sampling season and year, but precipitation was not measured on each individual site.

Vegetation on 12 study sites was sampled for frequency and yield during a 30-day period in July and August of 1982. To sample variability inherent within dry mountain meadows, four sites were selected from each of three range condition classes—good, fair, and poor. Condition was determined from USFS range analysis and trend study records. Study sites ranged in production from 512 to 1547 kg/ha. Botanical nomenclature followed Hitchcock and Cronquist (1973).

A 30.5 x 30.5-m frequency macroplot was established on each site in a topographically

uniform area with homogenous vegetation structure. This macroplot consisted of five parallel 30.5-m transect lines spaced 7.6 m apart. Rooted frequency of occurrence was recorded by species within 10x10-cm quadrats placed at 1.5-m intervals along the five transects: therefore, 100 frequency quadrats were measured per site. Quadrat size and sampling intensity were determined in a previous study (Mosley *et al.* 1986).

Yield was sampled within a 30.5 x 30.5-m Permanent Site Analysis Transect (PSAT) macroplot superimposed on the 30.5-m^2 frequency macroplot. This PSAT macroplot consisted of three parallel 30.5-m transect lines spaced 15.25 m apart. At 3.05-m intervals along the three transects, vegetation within a 0.29-m^2 circular plot was clipped and weighed by species. This procedure provided 30 yield plots per site (USDA no date). Dry weight determinations were made using conversion tables (USDA 1981).

Simple linear regression was used to estimate yield (kg/ha) from frequency (%) for each species encountered on four or more sites. Linear and quadratic models were evaluated.

Estimated total site yields were calculated by summing estimated individual species' yields. Only significant regression equations ($P < 0.10$) were used to estimate individual species' yields from frequency. Yields of species with a non-significant regression and of species sampled on less than four sites were estimated with that species' average yield over all sites on which it was sampled. Estimated total site yields were compared to actual total site yields with a paired t-test and regression analysis.

Results

The ranges of species' yield and frequency values sampled are shown in Table 1. Zero values are present because of the different quadrat size and placement used for sampling yield and frequency. For a site to be included in a species' regression, at least one non-zero value must have been recorded for either yield or frequency. Utilizing these data simple linear regressions between yield and frequency were significant ($P < 0.10$) for 21 of the 30 species (Table 2). Coefficients of determination were 0.70 or greater for 13 of these 21 species. Quadratic regressions also significantly related yield and frequency for 21 of the 30 species included in the analysis (Table 3), and

TABLE 1. Ranges of species' yield (kg/ha) and frequency values (%) for all sites.

Species	No. of sites	Range of Values	
		Yield	Frequency
Graminoids			
Agropyron dasystachyum	6	4- 81	2-43
Agropyron caninum	4	26- 80	6-21
Carex spp.	12	67-332	19-72
Danthonia intermedia	12	2-148	1-86
Deschampsia cespitosa	6	36-340	12-89
Festuca idahoensis	7	1-303	0-68
Juncus spp.	5	13-152	4-25
Koeleria cristata	6	3- 72	0-24
Muhlenbergia filiformis	6	0- 9	1-12
Stipa occidentalis	6	0- 87	1-13
Forbs			
Achillea millefolium	9	39-266	32-84
Agoseris glauca	6	9-159	0-32
Antennaria corymbosa	11	1- 19	0-20
Annual forbs	8	0- 26	1-69
Arabis spp.	4	0- 7	0- 3
Arenaria congesta	4	0- 36	1-27
Aster spp.	12	15-297	4-42
Calochortus nuttalli	8	3- 44	0-17
Camassia quamash	6	2-109	0-43
Cirsium vulgare	6	4-149	1-20
Delphinium nuttallianum	7	2- 36	0- 6
Gentiana calycosa	5	0- 86	1-11
Orthocarpus luteus	10	0- 40	0-12
Polygonum bistordies	4	3- 28	0- 5
Potentilla gracilis	4	2- 53	2-17
Ranunculus alismaefolius	4	0-123	1-39
Senecio integerrimus	8	2-265	1-29
Taraxacum officinale	4	10- 44	3-18
Trifolium longipes	11	3- 98	2-89
Wyethia helianthoides	7	0-142	0- 5

coefficients of determination were also 0.70 or greater for 13 of these species. Yield and frequency were not related in these models for eight species (Tables 2 and 3). It is not clear why these vegetation parameters were unrelated for these species.

Estimated total site yields did not differ ($P > 0.05$) from actual total site yields. This was true when either linear or quadratic models were used to estimate yield. The relationship between estimated and actual total site yield was linear (Figure 1). Our models tended to overestimate yield at the lower range of production (< 800 kg/ha) and underestimate actual yield at the higher levels of production.

Conclusions

Estimating herbaceous yield from species frequency appears promising. This study employed

TABLE 2. Coefficients of determination and linear regression equations relating yield (kg/ha) to frequency (x).

Species	r^2	Equation
Graminoids		
Agropyron dasystachyum	.74**	Y = 2.59 + 1.38x
Agropyron caninum	—	not significant
Carex spp.	.31*	Y = 44.84 + 2.16x
Danthonia intermedia	.92**	Y = 14.21 + 1.74x
Deschampsia cespitosa	.83**	Y = 4.71 + 4.15x
Festuca idahoensis	.91**	Y = −11.55 + 4.33x
Juncus spp.	.92**	Y = −7.21 + 6.65x
Koeleria cristata	.78**	Y = 3.32 + 2.79x
Muhlenbergia filiformis	—	not significant
Stipa occidentalis	—	not significant
Forbs		
Achillea millefolium	.56**	Y = −44.18 + 2.96x
Agoseris glauca	—	not significant
Antennaria corymbosa	.62**	Y = 2.42 + 0.70x
Annual forbs	.97**	Y = −1.15 + 0.39x
Arabis spp.	—	not significant
Arenaria congesta	.97**	Y = −2.74 + 1.41x
Aster spp.	.49**	Y = −0.35 + 4.87x
Calochortus nuttalli	.48*	Y = 3.86 + 1.58x
Camassia quamash	.94**	Y = 1.39 + 2.29x
Cirsium vulgare	—	not significant
Delphinium nuttallianum	.81**	Y = −2.56 + 5.43x
Gentiana calycosa	.74*	Y = 4.44 + 6.74x
Orthocarpus luteus	.46**	Y = 8.73 + 3.07x
Polygonum bistordies	.84*	Y = 3.43 + 4.02x
Potentilla gracilis	—	not significant
Ranunculus alismaefolius	—	not significant
Senecio integerrimus	.70**	Y = 13.13 + 8.58x
Taraxacum officinale	—	not significant
Trifolium longipes	.52**	Y = 11.43 + 0.60x
Wyethia helianthoides	.53*	Y = 9.79 + 19.79x

*Significant at $P < 0.10$

**Significant at $P < 0.05$

TABLE 3. Coefficients of determination and quadratic regression equations relating yield (kg/ha) to frequency (x).

Species	r^2	Equation
Graminoids		
Agropyron dasystachyum	.90**	$Y = 6.03 + 0.04x^2$
Agropyron caninum	—	not significant
Carex spp.	.34**	$Y = 81.60 + 0.02x^2$
Danthonia intermedia	.69**	$Y = 35.19 + 0.02x^2$
Deschampsia cespitosa	.69**	$Y = 93.84 + 0.04x^2$
Festuca idahoensis	.94**	$Y = 20.17 + 0.06x^2$
Juncus spp.	.87**	$Y = 27.31 + 0.22x^2$
Koeleria cristata	.72**	$Y = 11.28 + 0.11x^2$
Muhlenbergia filiformis	—	not significant
Stipa occidentalis	—	not significant
Forbs		
Achillea millefolium	.64**	$Y = 27.69 + 0.03x^2$
Agoseris glauca	—	not significant
Antennaria corymbosa	.47**	$Y = 4.33 + 0.03x^2$
Annual forbs	.93**	$Y = 1.44 + 0.01x^2$
Arabis spp.	—	not significant
Arenaria congesta	.99**	$Y = -0.10 + 0.05x^2$
Aster spp.	.39**	$Y = 46.19 + 0.09x^2$
Calochortus nuttalli	.45*	$Y = 7.73 + 0.08x^2$
Camassia quamash	.98**	$Y = 8.55 + 0.05x^2$
Cirsium vulgare	—	not significant
Delphinium nuttallianum	.96**	$Y = 1.95 + 0.92x^2$
Gentiana calycosa	—	not significant
Orthocarpus luteus	.33*	$Y = 12.39 + 0.21x^2$
Polygonum bistordies	.89*	$Y = 4.66 + 0.77x^2$
Potentilla gracilis	.82*	$Y = 8.20 + 0.15x^2$
Ranunculus alismaefolius	—	not significant
Senecio integerrimus	.54**	$Y = 51.76 + 0.25x^2$
Taraxacum officinale	—	not significant
Trifolium longipes	.50**	$Y = 17.31 + 0.01x^2$
Wyethia helianthoides	.65**	$Y = 19.00 + 4.32x^2$

*Significant at $P < 0.10$

**Significant at $P < 0.05$

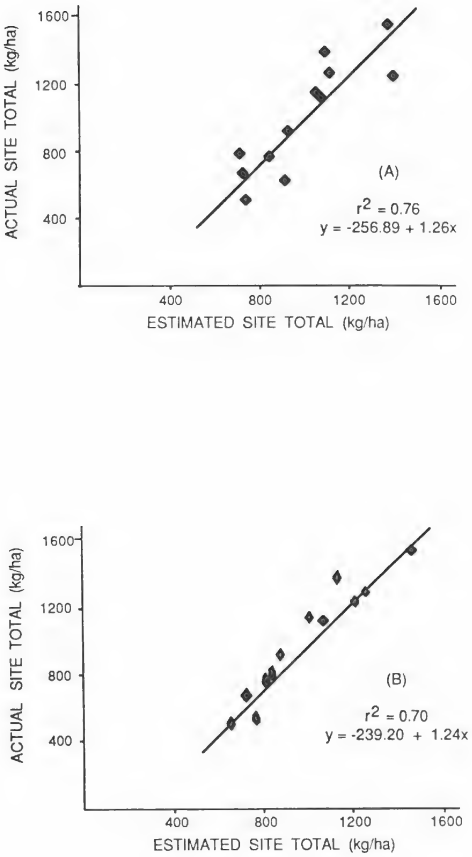

Figure 1. Relationship between estimated and actual total yields for 12 dry mountain meadow sites. Estimated site totals are the sum of individual species' estimates derived using linear (A) and quadratic (B) regression equations.

linear regression to develop significant ($P < 0.10$) equations for 21 species in dry mountain meadows of central Idaho. If yield and frequency were determined within the exact same quadrats, frequency-yield relationships should correlate even more closely. Both linear and quadratic equations were calculated; linear and quadratic models appeared equally appropriate. Selecting the better model depends upon which particular species are of special interest. Regression equations for individual species were used to estimate total yields for 12 mountain meadow sites. Estimated total yields did not differ ($P > 0.05$) from actual total yields.

Estimating yield from frequency data may have utility for monitoring key management species. Formulating regression equations for all species in many vegetation types may be time-prohibitive for most management applications. However, equations for one or two species per type could be developed relatively easily and inexpensively. Such yield information could be used to help set initial stocking levels. Managers should remember that it is impossible to precisely estimate carrying capacity from a single forage inventory because a site's herbaceous production varies with the amount and pattern of precipitation. Proper carrying capacity can best be determined by subsequently monitoring yield and species composition under the initial stocking level and making necessary adjustments in stocking rate.

A potential problem exists when relating frequency to yield. This is because frequency percentages are bounded variables whereas yield is an unbounded variable (Greig-Smith 1983). This potential problem reemphasizes the need to sample frequency with a proper quadrat size, one that provides intermediate frequency values which do not approach the bounded limits (Hyder *et al.* 1965). In addition to quadrat size, rooted frequency is also affected by the plant sizes, distributions, and densities present in a given community (Kershaw 1973). Relationships between species frequency and yield are thus specific to individual geographic areas and vegetation types. Therefore, different areas and different vegetation types would need their own regression equations. Equations presented here are specific for central Idaho's dry mountain meadows.

Finally, although species frequency is not largely influenced by temporal fluctuations in precipitation, herbaceous yield is greatly affected. Regression studies usually sample such variation by repeating measurements on the same site in different years. The effects of fluctuating precipitation levels can also be incorporated into regression equations by sampling several sites that differ widely in annual precipitation, provided that all of the sites are within the same community type. This study sampled dry mountain meadows receiving 510 to 1020 mm annual precipitation, varying from 512 to 1547 kg/ha herbaceous production.

Acknowledgements

Research was funded in part by USDA Science and Education Administration Grant No. 59-2161-1-2-082-0. This article is a joint contribution of the College of Agricultural Sciences, Texas Tech University, No. T-9-432, and Forest, Wildlife and Range Exp. Sta., University of Idaho, No. 288. The authors gratefully acknowledge Monte Miller of the Boise National Forest for his assistance with this study.

Literature Cited

Craddock, G. W. and C. L. Forsling. 1938. The influence of climate and grazing on spring-fall sheep range in southern Idaho. USDA Tech. Bull. 600.

Greig-Smith, P. 1983. Quantitative Plant Ecology. University of California Press, Berkeley.

Harris, R. W. 1954. Fluctuations in forage utilization on ponderosa pine ranges in eastern Oregon. J. Range Manage. 7:250-255.

Hitchcock, C. L. and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle.

Hyder, D. N., R. E. Bement, E. E. Remmenga, and C. Terwillger, Jr. 1965. Frequency sampling of blue grama range. J. Range Manage. 18:90-94.

Hyder, D. N., R. E. Bement, E. E. Remmenga, and C. Terwillger, Jr. 1966. Vegetation-soils and vegetation-grazing relations from frequency data. J. Range Manage. 19:11-17.

Kershaw, K. A. 1973. Quantitative and Dynamic Plant Ecology. William Clowes and Sons, London.

Mosley, J. C., S. C. Bunting, and M. Hironaka. 1986. Determining range condition from frequency data in mountain meadows of central Idaho. J. Range Manage. 39:561-565.

Odum, E. P. 1960. Organic production and turnover in old field succession. Ecology 41:34-39.

Smith, S. D. 1982. The frequency plot method as an improved technique for measuring successional trend. University of Idaho, Moscow. Thesis.

USDA. 1981. Forest Service (Region 4) Range Analysis Handbook. Amendment 11.

USDA. No date. The permanent site analysis transect method as a long-term trend study. Forest Service (R-4) Mimeo.

Received 3 March 1986
Accepted for publication 5 September 1986

W. G. Thies and **E. E. Nelson,** USDA Forest Service
Pacific Northwest Research Station, Forestry Sciences Laboratory
3200 Jefferson Way, Corvallis, Oregon 97331

Survival of Douglas-fir Injected with the Fumigants Chloropicrin, Methylisothiocyanate or Vorlex

Abstract

Most Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) trees injected with the fumigants chloropicrin, methylisothiocyanate (MIT), or Vorlex were alive and growing 2 and 3 years following treatment. Fumigants were introduced through holes drilled near the base of the tree down into the root collar; the dosages approximated and bracketed those shown earlier to eradicate *Phellinus weirii* (Murr.) Gilb. from infested stumps and roots of harvested trees. After 3 growing seasons, 21 of 45 treated with chloropicrin and all 45 trees treated with MIT were still living. After two growing seasons, the crown condition of trees treated with Vorlex were found to be poorer than crowns of check trees while the crowns of trees treated with MIT were about the same as those of check trees. Although all the fumigants tested are broad spectrum biocides, most Douglas-fir survived the treatments at dosages previously demonstrated to eradicate *P. weirii* from stumps. Conventional wisdom regarding the use of phytotoxic chemicals to control plant pathogens may not always apply when application is made to the heartwood of a tree.

Introduction

Phellinus weirii (Murr.) Gilb., cause of laminated root rot, infects nearly all commercially important conifer species in western North America, where it reduces forest productivity by about 4.4 million m^3 annually (Nelson *et al.* 1981). The disease, its distribution and impact, and current research on control have been discussed previously (Hadfield 1985, Nelson *et al.* 1981, Thies 1984).

Several soil fumigants have been reported to eradicate fungi from utility poles (Graham and Corden 1980), from infested wood buried in soil when applied to soil (Bliss 1951, Godfrey 1936, Houston and Eno 1969), and from stumps when placed in stumps (Filip and Roth 1977, Thies and Nelson 1982). Live Douglas-fir were shown to tolerate chloropicrin internally when eight chloropicrin-treated trees remained alive after 4 years and were reported to have growth comparable to that of control trees (Goodell *et al.* 1984).

The discoveries that chloropicrin could be used to eradicate *P. weirii* from infested stumps and roots and that trees can survive injection with this fumigant suggested the possibility of therapeutic application of fumigants to Douglas-fir infected by *P. weirii.* A major question remains: Can trees tolerate levels of fumigant necessary to kill wood-inhabiting fungi in roots and stems? In this paper we report findings 30 months (three growing seasons) after injecting Douglas-fir with the fumigants chloropicrin[1] or methylisothiocyanate (MIT), and 17 months (two growing seasons) after injecting Douglas-fir with Vorlex (v/v 20 percent MIT, 80 percent chlorinated C_3 hydrocarbons) and chloropicrin. Survival of the fungus, requiring destructive sampling of trees, can be determined only at the conclusion of this long term study or as individual trees die.

Methods and Materials

The study area, in the Oregon Coast Ranges near Apiary, Oregon (46° 1' N. latitude, 123° 4' W. longitude), had the following characteristics: elevation 420 m, slope 0-35 percent, mean annual precipitation 145 cm (U.S. Weather Bureau 1965), and Olympic silt loam soil. The 47-year-old, naturally regenerated stand of predominantly Douglas-fir growing on the site indicated a rating of site II (McArdle *et al.* 1949). Only dominant and codominant Douglas-fir, with clearly visible crowns, were selected for fumigation. Trees showing severe distress symptoms were rejected.

Selection of trees

Because tolerance to fumigants could depend upon presence and cause of stem and root decay, we selected trees in 3 classes of probable decay

[1]This paper reports the results of research only. Mention of a pesticide does not constitute a recommendation for use by the U.S. Department of Agriculture, nor does it imply registration under The Federal Insecticide, Fungicide, and Rodenticide Act as amended. Also, mention of a commercial or proprietary product does not constitute recommendation or endorsement by the U.S. Department of Agriculture.

caused by *P. weirii.* Candidate trees were examined for the presence of *P. weirii* by carefully exposing major lateral roots within 60 cm of the base of the tree, examining the root surface for characteristic ectotrophic mycelium, and boring with an increment borer to detect stained or decayed root wood. Each tree was tagged, and measured, then, based on examination results, assigned to one of three infection classes: I, Infected; II, Probably infected, with crown symptoms and inoculum within 5 m but *P. weirii* not found on subject tree; III, Probably uninfected, no symptoms and no identified inoculum source within 25 m of subject tree.

Each infection class contained 45 trees separated into 5 groups of 9 based on similarities of diameter at breast height (dbh) and tree location. Selected trees ranged in dbh from 27.4 cm to 62.2 cm. Treatments were randomly assigned to trees within each group. Crown condition of individual trees was not recorded prior to treatment. As a result of the blocking and random assignment of treatments within blocks, we assumed that the average crown condition for the trees in each treatment was the same at the time of treatment.

Treatments

One of nine treatments was applied to each tree in the study: chloropicrin and MIT were applied at several dosages, and Vorlex was applied at a single dosage. Both chloropicrin and Vorlex have been shown to eradicate *P. weirii* from infested stumps (Thies and Nelson 1982). MIT is an ingredient in Vorlex. At room temperature Vorlex and chloropicrin are liquids, whereas MIT is a white, waxy solid. Holes drilled in the trees to apply the fumigant were part of the treatment. Check trees had neither holes drilled nor fumigants applied.

Test dosages were based on a dosage expected to kill *P. weirii* in treated wood. Earlier work (Thies and Nelson 1982) suggested that a dose of 6.7 ml of either chloropicrin or Vorlex per kg of stump and root biomass was sufficient to eradicate *P. weirii.* For this study, a standard dosage (D) was 6.7 ml of chloropicrin, or 6.7 ml of Vorlex or 1.5 g of MIT per kg of treated biomass. The dosage for MIT was based on the concentration of MIT in Vorlex (232 g MIT per 1.0 l Vorlex). For ease of application, the dosages were rounded upward to the next quarter liter of chloropicrin or Vorlex and to the next even increment of 58 g of MIT. We assumed that the dose tolerated by a tree would vary linearly with the estimated biomass of its major roots and lower bole. The dose applied to each tree was based on treated biomass, estimated from the dbh. The nine treatments were defined in terms of standard dosages (Table 1).

TABLE 1. Number of live study trees and crown rating in mid-September 1984, following treatment with 3 fumigants in living Douglas-fir in western Oregon.

Treatment	Live trees[a]	Frequency of trees by Crown-Condition[b] 0	1-3	4-6	7-9	10
Applied March 1982:						
Check	14	1	1	—	8	5
Chloropicrin 1D[c]	3	12	1	—	2	—
Chloropicrin 0.5D	6	9	3	—	3	—
Chloropicrin 0.25D	12	3	5	1	6	—
MIT D	15	—	—	—	13	2
MIT 0.5D	15	—	—	—	13	2
MIT 0.25D	15	—	—	—	9	6
Applied April 1983:						
Chloropicrin 0.125D	15	—	—	—	13	2
Vorlex 0.5D	14	1	4	3	6	1

[a]Number of live trees remaining out of 15 trees treated.

[b]Crown-Condition rating of live trees. Based on an 11-point scale where 0 = dead and 10 = vigorous.

[c]D = standard dosage of 6.7 ml of chloropicrin or Vorlex, or 1.5 g of MIT per kg of treated biomass.

Each of the 9 treatments was applied to 15 trees, 5 trees in each of 3 infection classes. Treatments were applied in March 1982, except for chloropicrin 0.125D and Vorlex 0.5D, which were applied in April 1983.

Estimating biomass of wood treated

Based on fumigant movement of 2.4 m or more in poles (Graham and Cordon 1980) at wood moisture contents of about 30 to 40 percent (ovendry weight)—which is typical of heartwood of living Douglas-fir trees (Forest Products Laboratory 1973), we assumed that fumigant vapors would diffuse 2.4 m from the application holes.

We estimated treated biomass by 2.5-cm dbh classes from the following relationships: (1) Stem biomass (to 2.4-m height): $Y = 0.0007128 + 0.0002716\ X$; where Y = stem volume in m^3, X = basal area (breast high) in cm^2 ($n = 47$, $r^2 = 0.993$; sample trees ranged from 17.0- to 61.7-cm dbh). Data were from Douglas-fir in a single stand in the Coast Ranges near Apiary, Oregon (Thies, unpublished data). (2) Below ground stem and root biomass: $\ln Y = -4.6961 + 2.6929 \ln X$; where Y = below ground biomass in kg, X = dbh in cm, ln = logarithms to the base e ($n = 26$, $r^2 = 0.96$; trees ranged from 2.3- to 23.0-cm dbh and from 94- to 135-cm dbh). Biomass was based on all roots having a diameter equal to or greater than 10 mm. Data were from two stands on the west slope of the Cascade Range (Gholz *et al.* 1979). Wood density was assumed to be 0.44 g per cm^3. For example: a small tree with a dbh of 15 cm has an estimated treatable biomass of 34 kg and would receive a D dose of 0.25 l of chloropicrin or Vorlex, or 58 g of MIT; a large tree with a dbh of 60 cm has an estimated treatable biomass of 898 kg and would receive a D dose of 6.0 l chloropicrin or Vorlex, or 1362 g of MIT.

Application of fumigants

A series of equally spaced 3.2-cm-diameter holes was drilled in each tree receiving fumigant. Holes were drilled at approximately a 45-degree angle below horizontal and extending past the center of the tree. For the lowest dosage the holes were equally spaced around the tree approximately 30 cm above the litter layer. For larger dosages the holes were drilled 15 cm apart on a spiral that started approximately 15 cm above the litter layer and moved approximately 30 cm up the bole with each turn around the tree, for a maximum of two turns. A dose of chloropicrin or Vorlex was distributed (poured) equally into all holes in a tree; MIT was applied as a solid in small polyethylene sacks. Each sack was broken as it was pushed into a hole. Each hole was tightly plugged with a 12.5-cm-long by 3.3-cm-diameter hemlock dowel. Plugs were beveled at one end to facilitate driving them into the holes, then the beveled end was dipped into resorcinol glue (to resist passage of the fumigant through the dowel) and allowed to harden before use.

Data collection

The crown of each study tree was examined, photographed, and visually rated in mid-August 1982, mid-September 1983, and mid-September 1984. Particular note was made of crown condition. Crowns were rated on an 11-point scale of crown condition (C-C), from dead (0) to vigorous (10). The rating was based on needle complement, needle length and color, number and distribution of dead needles and branches, internodal growth, and number and growth of new branches.

In October 1983 and September 1984 dead subject trees were felled and their stumps and roots removed and cleaned. All roots recovered were cut at 30-cm intervals. When stain or decay typical of *P. weirii* infection was found a 5-cm thick disk was removed. Each disk was split longitudinally and five chips were removed aseptically from the split face in areas of typical stain or advanced decay and placed on 1.5% malt agar slants in culture tubes. Culture tubes were incubated for 14 days at room temperature. Presence of *P. weirii* was determined from morphological features of developing colonies (Nelson 1975).

Results

Of 120 Douglas-fir treated with fumigants, 95 trees were still alive at the time of our evaluation in mid-September 1984. After three growing seasons (30 months), trees treated in March 1982 showed differences in crown condition among treatments. At the end of the first growing season there were no dead trees and only relatively minor indications of a decline in crown condition, but by the end of the second growing season, 22 trees had died and differences among treatments in appearance of the crowns had become evident. By the end of the third growing season 25 treated trees were dead (Table 1) but crowns of remaining trees showed little change in crown condition from the second growing season.

All trees treated with 0.5D Vorlex or 0.125D chloropicrin in April 1983 were alive in September 1983. After one growing season, crowns of Vorlex-treated trees but not chloropicrin-treated trees were rated as less vigorous than crowns of check trees. At the end of the second growing season crown condition of chloropicrin-treated trees and check trees was unchanged. Trees treated with Vorlex had average crown ratings lower than checks and one of the 15 treated trees was dead. Vorlex at 0.5D and MIT

at 0.5D (administered 1 year earlier), contained the same amount of MIT, but after three growing seasons all 15 trees receiving MIT at 0.5D were alive and they had better C-C ratings than trees receiving Vorlex at 0.5D.

We can draw conclusions about the relative toxicity of the chemicals to the trees; however, since we have not examined the roots of the living treated trees, we are unable to determine if dosages non-lethal to trees were effective in killing wood inhabiting fungi.

Isolations attempted from stumps and roots of 26 dead trees recovered *P. weirii* from all disks from the check tree, but from only 22 percent of the root disks from the 25 chloropicrin- or Vorlex-treated trees. However, since we have not examined the roots of 94 of the treated trees we are unable to compare the individual treatments based on reduced viability of *P. weirii* inoculum.

We did not find meaningful differences in mortality or crown conditions among infection classes.

Discussion

Although all the fumigants are toxic, broad spectrum biocides, 73 percent of the treated trees were still living three growing seasons after treatment. Chloropicrin appeared more toxic to Douglas-fir than MIT: of 25 treated trees that died, 24 were treated with chloropicrin and there had been a decline in the crown condition of surviving trees. In contrast, after three growing seasons the crown condition of MIT-treated trees did not appear different from the check trees.

Although limited to two seasons of exposure, crown condition of check trees was similar to trees treated with chloropicrin at the lowest dosage (0.125D). This dosage approximates the highest dosage tested in an earlier study (Goodell *et al.* 1984) in which eight chloropicrin-treated healthy Douglas-fir survived and attained growth comparable to check trees 4 years after treatment.

For a given dosage of MIT, there was more adverse impact on Douglas-fir if the fumigant was delivered as Vorlex rather than as MIT. Because we did not apply the Vorlex carrier as a treatment without the MIT, we cannot rule out the possibility of a synergistic effect on the tree. Nevertheless, if our primary goal is to maintain or improve the health of the tree, and the stand in general, then MIT alone was less harmful.

Although limited to the roots of killed trees, isolation results confirmed that fumigants can reduce *P. weirii* in roots of Douglas-fir trees as well as stumps. A comparison of treatment effectiveness will not be possible until all trees in the study can be felled and their roots examined.

The results from this study suggest that host trees can be treated with fumigant in quantities large enough to expect a reduction in inoculum potential of a root rot pathogen without killing the host. These results encourage additional research to identify other potential fumigants and to determine the efficacy of any fumigant to reduce residual inoculum.

Acknowledgements

Our thanks to K. C. VanNatta of Rainier, Oregon, for providing study trees, equipment, and personal services. We also thank NOR-AM Agricultural Products, Inc. (Naperville, Illinois) and Great Lakes Chemical Corporation (Fresno, California) for supplying fumigants, advice, and financial assistance. Our appreciation goes to Dr. R. D. Graham, Dr. M. E. Corden, and B. G. Goodell (Oregon State University, Corvallis, Oregon) for advice, to Harlan Fay for technical support, and to Joe McNeil and Michael McWilliams for field assistance.

Literature Cited

Bliss, D. E. 1951. The destruction of *Armillaria mellea* in citrus soils. Phytopathology 41:665-683.

Filip, G. M., and L. F. Roth. 1977. Stump injections with soil fumigants to eradicate *Armillariella mellea* from young growth ponderosa pine killed by root rot. Can. J. For. Res. 7:226-231.

Forest Products Laboratory. 1973. Veneer species of the world. USDA For. Serv., For. Prod. Lab., Madison, *Wisconsin*.

Gholz, H. L., C. C. Grier, A. G. Campbell, and A. T. Brown. 1979. Equations for estimating biomass and leaf area of plants in the Pacific Northwest. For. Res. Lab. Pap. 41, Oregon State Univ., Corvallis, Oregon.

Godfrey, G. H. 1936. Control of soil fungi by soil fumigation with chloropicrin. Phytopathology 25:246-256.

Goodell, B. S., G. S. Helsing, and R. D. Graham. 1984. Responses of Douglas-fir trees to injection of chloropicrin. Can. J. For. Res. 14:623-627.

Graham, R. D., and M. E. Corden. 1980. Controlling biological deterioration of wood with volatile chemicals. Elec. Power Res. Inst. EL-1480, Proj. 212-1. Elec. Power Res. Inst., Palo Alto, Calif.

Hadfield, J. S. 1985. Laminated root rot, a guide for reducing and preventing losses in Oregon and Washington forests. USDA For. Serv., Pac. Northw. Reg., Portland, Oregon.

Houston, D. R. and H. G. Eno. 1969. Use of soil fumigants to control spread of *Fomes annosus*. USDA For. Serv. Res. Pap. NE-123 Northeast. For. Exp. Stn., Broomall, Pennsylvania.

McArdle, R. E., W. H. Meyer, and D. Bruce. 1949. The yield of Douglas-fir in the Pacific Northwest. U.S. Dep. Agric. Tech. Bull. No. 201 Washington, D.C.

Received 30 April 1986
Accepted for publication 22 September 1986

Nelson, E. E. 1975. Survival of *Poria weirii* on paired plots in alder and conifer stands. Microbios 12:155-158.

Nelson, E. E., N. E. Martin, and R. E. Williams. 1981. Laminated root rot of western conifers. For. Insect and Dis. Leaf. 159 USDA For. Serv. Washington, D.C.

Thies, W. G. 1984. Laminated root rot: The quest for control. J. For. 82:345-356.

Thies, W. G., and E. E. Nelson. 1982. Control of *Phellius weirii* in Douglas-fir stumps by the fumigants chloropicrin, allyl alcohol, Vapam, and Vorlex. Can. J. For. Res. 12:528-532.

U.S. Weather Bureau. 1965. Climatic summary of the United States. Supplement for 1951 through 1960, Oregon. Climatographs of the United States 86-31.

Northwest Science
Volume 60 (1986)
Author and Subject Index

(Author headings are in capital letters)

Abies *see* firs
ALABACK, P. B. Biomass regression equations for understory plants in coastal Alaska: effects of species and sampling design on estimates. 90-103
Alaska
forest biomass estimates: Alaback, 90-103
plant distributions: Odasz, 104-107
ANDERSON, J. E. *see* Shumar and Anderson, 179-185
Anoplarchus *see* stichaeoid fish
archaeology
obsidian artifacts: Hughes, 73-80
Ardea *see* herons
Artemisia *see* sagebrush
ARTHUR, W. J., III and D. H. JANKE. Radionuclide concentrations in wildlife occurring at a solid radioactive waste disposal area. 154-159
ash, volcanic
at Battle Ground Lake: Juvigné, 210-217
and salmon: Kirn, Ledgerwood and Jensen, 191-196
and zooplankton: Gaddy and Parker, 47-51
Astragalus *see* milkvetch

BARTON, M. Influence of substratum on the comparative food habits of two species of estuarine stichaeoid fishes, *Anoplarchus purpurescens* (Family Stichaeidae) and *Pholis ornata* (Family Pholididae). 125-130
bats
little brown (*Myotis lucifugus*): Lunde and Harestad, 206-209
Battle Ground Lake, Wa
sediments: Juvigné, 210-217
bears
black (*Ursus americanus*) and grizzly (*U. arctos*) in Washington: Lyman, 67-72
BELL, M. A. M. *see* Fyles and Bell, 8-14
bentonite mine spoils
and deer mice: Sieg, Uresk and Hansen, 81-89
and small mammals: Sieg, Uresk and Hansen, 218-224
biomass estimates
in forests: Alaback, 90-103
birds
bald eagle perch sites: Fielder and Starkey, 186-190
flammulated owls: Hayward, 141-144
great blue herons: Julin, 201-205
and radionuclides: Arthur and Janke, 154-159
wild turkey brood habitats: Mackey, 108-112
wintering passerines: Tank and Sidle, 238-242
BLAHM, T. H. *see* McCabe, Emmett, Muir and Blahm, 113-124
British Columbia
little brown bats: Lunde and Harestad, 206-209
river bars and plants: Fyles and Bell, 8-14
sedge germination: Hutchinson and Smythe, 36-41
Brooks Range, Al
plant distributions: Odasz, 104-107
BUNTING, S. C. *see* Smith, Bunting and Hironaka, 279-286
BUTLER, D. R. Conifer invasion of subalpine meadows, central Lemhi Mountains, Idaho. 166-173

CAMERON, K. A. and P. PRINGLE. Post-glacial lahars of the Sandy River basin, Mount Hood, Oregon. 225-237
Carex *see* sedges
Cascade Mountains, Wa
alpine plants and pollination: Shaw and Taylor, 21-31
Cervus *see* elk
CHISHOLM, I. M. and W. A. HUBERT. Influence of stream gradient on standing stock of brook trout in the Snowy Range, Wyoming. 137-139
Clethrionomys *see* voles
Columbia River
chinook salmon: McCabe, Emmett, Muir and Blahm, 113-124
chinook salmon and ash: Kirn, Ledgerwood and Jensen, 191-196
squawfish: Kirn, Ledgerwood and Nelson, 197-200
Compositae *see* sagebrush
conifers *see* Pinaceae
count marks
in rock art: Lewis, 243-249
CROSS, S. P. *see* Hayes, Cross and McIntire, 250-257
CUDMORE, W. W. Ectoparasites of *Neotoma cinerea* and *N. fuscipes* from western Oregon. 174-178
Cyperaceae *see* sedges

deer
mule (*Odocoileus hemionus*) and selenium: Fielder, 15-20
DEMARTINI, E. E. Reproductive colorations, paternal behavior and egg masses of kelp greenling, *Hexagrammos decagrammus,* and whitespotted greenling, *H. stelleri.* 32-35
DOESCHER, P. S., R. F. MILLER, S. R. SWANSON and A. H. WINWARD. Identification of the *Artemisia tridentata* spp *wyomingensis/Festuca idahoensis* habitat type in eastern Oregon. 55-60
douglas-firs
(*Pseudotsuga menziesii*) and blue herons: Julin, 201-205
meadow invasion: Butler, 166-173
seedling temperature tolerance: Seidel, 1-7
see also firs
DUNCAN, S. H. Peak stream discharge during thirty years of sustained yield timber management in two fifth order watersheds in Washington state. 258-264

eagles
bald (*Haliaeetus leucocephalus*) perch sites: Fielder and Starkey, 186-190
ecology
and environmental problem-solving: Orians, 287-292
ectoparasites
on woodrats: Cudmore, 174-178
elk
Rocky Mountain (*Cervus elaphus nelsoni*) and selenium: Fielder, 15-20
EMMETT, R. L. *see* McCabe, Emmett, Muir and Blahm, 113-124
environmental problems
and solutions: Orians, 287-292

fescue
Idaho (*Festuca idahoensis*): Doescher, Miller, Swanson and Winward, 55-60
Festuca *see* fescue
FIELDER, P. C. Implications of selenium levels in Washington mountain goats, mule deer and Rocky Mountain elk. 15-20
FIELDER, P. C. and R. G. STARKEY. Bald eagle perch-sites in eastern Washington. 186-190
firs
grand (*Abies grandis*) and root trenching: McCune, 52-54
grand (*A. grandis*) and seedling temperature tolerance: Seidel, 1-7
see also douglas-firs
fish
brook trout and stream gradients: Chisholm and Hubert, 137-139
chinook salmon diet: Kirn, Ledgerwood and Jensen, 191-196
chinook salmon diet: McCabe, Emmett, Muir and Blahm, 113-124
greenling reproductive behavior: DeMartini, 32-35
squawfish abundance, Kirn, Ledgerwood and Nelson, 197-200
stichaeoid fish diet: Barton, 125-130
forests
biomass estimates: Alaback, 90-103
conifer seedling temperature tolerance: Seidel, 1-7
conifers and grasses: McDonald, 271-278
and great blue herons: Julin, 201-205
and little brown bats: Lunde and Harestad, 206-209
and meadow invasion: Butler, 166-173
and root competition: McCune, 52-54
timber management and streams: Duncan, 258-264
frequency plots
and vegetation changes: Smith, Bunting and Hironaka, 279-286
FYLES, J. W. and M. A. M. BELL. Vegetation colonizing river gravel bars in the Rocky Mountains of southeastern British Columbia. 8-14

GADDY, A. J. and R. A. PARKER. Zooplankton grazing activity and assimilation in the presence of Mount St. Helens ash. 47-51
geochemistry
obsidian: Hughes, 73-80
geology
late-Quaternary sediments: Juvigné, 210-217
post-glacial lahars: Cameron and Pringle, 225-237
sedimentary rocks of Manastash Formation: Lewellen, 160-165
geomorphology
Whatcom County, Washington: Goldin, 61-66
germination
and salinity: Hutchinson and Smythe, 36-41
goats
mountain (*Oreamnos americanus*) aerial census: Houston, Moorhead and Olson, 131-136
mountain (*O. americanus*) and selenium: Fielder, 15-20
GOLDIN, A. Geomorphic surfaces and soils, northwestern Whatcom County, Washington. 61-66
Gramineae *see* fescue, grasses
grasses
and young conifers: McDonald, 271-278
gravel bars
and plant communities: Fyles and Bell, 8-14
greenling
kelp (*Hexagrammos decagrammus*) and whitespotted (*H. stelleri*): DeMartini, 32-35

Haliaeetus *see* eagles
HANSEN, R. M. *see* Sieg, Uresk and Hansen, 81-89, 218-224
HARESTAD, A. S. *see* Lunde and Harestad, 206-209
HAYES, J. P., S. P. CROSS and P. W. MCINTIRE. Seasonal variation in mycophagy by the western red-backed vole, *Clethrionomys californicus,* in southwestern Oregon. 250-257
HAYWARD, G. Activity pattern of a pair of nesting flammulated owls (*Otus flammeolus*) in Idaho. 141-144
heat tolerance
in conifer seedlings: Seidel, 1-7
herons
great blue (*Ardea herodias*) and nesting trees: Julin, 201-205
Hexagrammos *see* greenling
HIRONAKA, M. *see* Smith, Bunting and Hironaka, 279-286
HOUSTON, D. B., B. B. MOORHEAD and R. W. OLSON. An aerial census of mountain goats in the Olympic Mountain range, Washington. 131-136
HUBERT, W. A. *see* Chisholm and Hubert, 137-139
HUGHES, R. E. Energy dispersive X-ray fluorescence analysis of obsidian from Dog Hill and Burns Butte, Oregon. 73-80
HUTCHINSON, I. and S. R. SMYTHE. The effect of antecedent and ambient salinity levels on seed germination in populations of *Carex lyngbyei* Hornem. 36-41

Idaho
conifer invasion of meadows: Butler, 166-173
flammulated owls: Hayward, 141-144
radioactive waste and wildlife: Arthur and Janke, 154-159
sagebrush and sand dunes: Shumar and Anderson, 179-185
wintering passerine birds: Tank and Sidle, 238-242
insects
and milkvetch seeds: Youtie and Miller, 42-46

JANKE, D. H. *see* Arthur and Janke, 154-159
JENSEN, A. L. *see* Kirn, Ledgerwood and Jensen, 191-196
JULIN, K. R. Decline of second-growth Douglas-fir in relation to great blue heron nesting. 201-205
JUVIGNE, E. H. Late-Quaternary sediments at Battle Ground Lake, southern Puget Trough, Washington. 210-217.
KIRN, R. A., R. D. LEDGERWOOD and A. L. JENSEN. Diet of subyearling chinook salmon (*Oncorhynchus tshawytscha*) in the Columbia River estuary and changes effected by the 1980 eruption of Mount St. Helens. 191-196
KIRN, R. A., R. D. LEDGERWOOD and R. A. NELSON. Increased abundance and the food consumption of northern squawfish (*Ptychocheilus oregonensis*) at River Kilometer 75 in the Columbia River. 197-200

lahars
post-glacial: Cameron and Pringle, 225-237
LEDGERWOOD, R. D. *see* Kirn, Ledgerwood and Jensen, 191-196 and Kirn, Ledgerwood and Nelson, 197-200
Leguminosae *see* milkvetch
Lemhi Mountains, Id
conifer invasion of meadows: Butler, 166-173
LEWELLEN, D. G. Petrographic differences between two sedimentary rock bodies of the Eocene-age Manastash Formation, Kittitas County, Washington. 160-165
LEWIS, T. H. Counts, coups and tally marks: evidence of notational systems in the pictographic/petroglyphic record. 243-249

LUNDE, R. E. and A. S. HARESTAD. Activity of little brown bats in coastal forests. 206-209
LYMAN, R. L. On the Holocene history of *Ursus* in eastern Washington. 67-72

MCCABE, G. T., JR., R. L. EMMETT, W. D. MUIR and T. H. BLAHM. Utilization of the Columbia River estuary by subyearling chinook salmon. 113-124
MCCUNE, B. Root competition in a low-elevation grand fir forest in Montana—a trenching experiment. 52-54
MCDONALD, P. M. Grasses in young conifer plantations—hindrance and help. 271-278
MCINNIS, M. L. and M. VAVRA. Summer diets of domestic sheep grazing mountain meadows in northeastern Oregon. 265-270
MCINTIRE, P. W. *see* Hayes, Cross and McIntire, 250-257
MACKEY, D. L. Brood habitat of Merriam's turkeys in south-central Washington. 108-114
mammals
  see bears, deer, elk, goats, sheep
mammals, small
  bat activity: Lunde and Harestad, 206-209
  and bentonite mine spoils: Sieg, Uresk and Hansen, 218-224
  deer mice diets: Sieg, Uresk and Hansen, 81-89
  mycophagy: Rhoades, 150-153
  mycophagy and voles: Hayes, Cross and McIntire, 250-257
  and radionuclides: Arthur and Janke, 154-159
  on uranium mill tailings: Rumble, 145-149
  woodrat ectoparasites: Cudmore, 174-178
Manastash Formation, Wa
  sedimentary rocks: Lewellen, 160-165
marshes
  sedge germination and salinity: Hutchinson and Smythe, 36-41
Meleagris *see* turkeys
mice
  deer (*Peromyscus maniculatus*) diets: Sieg, Uresk and Hansen, 81-89
milkvetch
  threadsilk (*Astragalus filipes*) and woolly-pod (*A. purshii*) pollination: Youtie and Miller, 42-46
MILLER, R. F. *see* Doescher, Miller, Swanson and Winward, 55-60, and Youtie and Miller, 42-46
Montana
  deer mice diets: Sieg, Uresk and Hansen, 81-89
  petroglyphic count marks: Lewis, 243-249
  root competition in forests: McCune, 52-54
  small mammals on bentonite mine spoils: Sieg, Uresk and Hansen, 218-224
MOORHEAD, B. B. *see* Houston, Moorhead and Olson, 131-136
Mount Hood, Or
  post-glacial lahars: Cameron and Pringle, 225-237
Mount St. Helens, Wa
  ash and salmon: Kirn, Ledgerwood and Jensen, 191-196
  ash and zooplankton: Gaddy and Parker, 47-51
  eruption and squawfish: Kirn, Ledgerwood and Nelson, 197-200
MUIR, W. D. *see* McCabe, Emmett, Muir and Blahm, 113-124
mycophagy
  in small mammals: Rhoades, 150-153
  in voles: Hayes, Cross and McIntire, 250-257
Myotis *see* bats

NELSON, R. A. *see* Kirn, Ledgerwood and Nelson, 197-200
Neotoma *see* woodrats
notational systems
  in rock art: Lewis, 243-249
nuclear waste
  in mill tailings: Rumble, 145-149
  and wildlife: Arthur and Janke, 154-159

obsidian
  in archaeological artifacts: Hughes, 73-80
ODASZ, A. M. Distributions of 40 rare vascular plants in the Alatna River drainage of the central Brooks Range, Alaska. 104-107
Odocoileus *see* deer
OLSON, R. W. *see* Houston, Moorhead and Olson, 131-136
Olympic Mountains, Wa
  mountain goats: Houston, Moorhead and Olson, 131-136
Oncorhynchus *see* salmon
Oreamnos *see* goats
Oregon
  domestic sheep diets: McInnis and Vavra, 265-270
  ectoparasites on woodrats: Cudmore, 174-178
  insects and milkvetch: Youtie and Miller, 42-46
  obsidian: Hughes, 73-80
  post-glacial lahars: Cameron and Pringle, 225-237
  sagebrush/fescue habitat: Doescher, Miller, Swanson and Winward, 55-60
  squawfish abundance: Kirn, Ledgerwood and Nelson, 197-200
  voles and mycophagy: Hayes, Cross and McIntire, 250-257
ORIANS, G. H. Ecology and environmental problem-solving. 287-292
Otus *see* owls
Ovis *see* sheep
owls
  flammulated (*Otus flammeolus*) in Idaho: Hayward, 141-144

PARKER, R. A. *see* Gaddy and Parker, 47-51
passerine birds
  wintering in Idaho: Tank and Sidle, 238-242
  see also birds
Peromyscus *see* mice
petroglyphs
  countmarks: Lewis, 243-249
Pholis *see* stichaeoid fish
Picea *see* spruce
Pinaceae
  and grasses: McDonald, 271-278
  invasion of meadows: Butler, 166-173
  see also douglas-firs, firs, pines, spruce
pines
  lodgepole (*Pinus contorta*) and limber (*P. flexilis*) in meadow invasion: Butler, 166-173
  ponderosa (*P. ponderosa*) seedling tolerance: Seidel, 1-7
plant communities
  biomass estimates: Alaback, 90-103
  conifer invasion: Butler, 166-173
  detecting vegetation change: Smith, Bunting and Hironaka, 279-286
  on gravel bars: Fyles and Bell, 8-14
  and pollination: Shaw and Taylor, 21-31
  sagebrush: Shumar and Anderson, 179-185
  sagebrush/grassland: Doescher, Miller and Winward, 55-60
  sedges: Hutchinson and Smythe, 36-41
plant distributions
  Alaska: Odasz, 104-107
pollination
  and alpine fell-field community: Shaw and Taylor, 21-31
PRINGLE, P. *see* Cameron and Pringle, 225-237

Pseudotsuga *see* douglas-firs
Ptychocheilus *see* squawfish

radiation exposure
of small mammals: Rumble, 145-149
radioactive waste disposal
and wildlife: Arthur and Janke, 154-159
RHOADES, F. Small mammal mycophagy near wood debris accumulations in the Stehekin River valley, Washington, 150-153
rivers
plants on gravel bars: Fyles and Bell, 8-14
Rocky Mountains, B.C.
river bars and plants: Fyles and Bell, 8-14
RUMBLE, M. A. Radiation dosimetry on revegetated uranium mill tailings in western South Dakota. 145-149
ruminants
and selenium: Fielder, 15-20
see also deer, elk, goats

sagebrush
big (*Artemisia tridentata*) on sand dunes: Shumar and Anderson, 179-185
Wyoming big (*A. tridentata* ssp. *wyomingensis*) in Oregon: Doescher, Miller, Swanson and Winward, 55-60
salmon
chinook (*Oncorhynchus tshawytscha*) diet: Kirn, Ledgerwood and Jensen, 191-196
chinook (*O. tshawytscha*) in Columbia River estuary: McCabe, Emmett, Muir and Blahm, 113-124
Salvelinus *see* trout
sand dunes
and sagebrush: Shumar and Anderson, 179-185
sedges
Carex lyngbyei and salinity: Hutchinson and Smythe, 36-41
sediments
at Battle Ground Lake: Juvigné, 210-217
SEIDEL, K. W. Tolerance of seedlings of ponderosa pine, douglas-fir, grand fir and Engelmann spruce for high temperatures. 1-7
selenium
in goats, deer and elk: Fielder, 15-20
SHAW, D. C. and R. J. TAYLOR. Pollination ecology of an alpine fell-field community in the north Cascades. 21-31
sheep
domestic (*Ovis aries*) diets: McInnis and Vavra, 265-270
SHUMAR, M. L. and J. E. ANDERSON. Water relations of two subspecies of big sagebrush on sand dunes in southeastern Idaho. 179-185
SIDLE, W. B. *see* Tank and Sidle, 238-242
SIEG, C. H., D. W. URESK and R. M. HANSEN. Seasonal diets of deer mice on bentonite mine spoils and sagebrush grasslands in southeastern Montana. 81-89
The value of bentonite mine spoils in southeastern Montana as small mammal habitat. 218-224
SMITH, S. D., S. C. BUNTING and M. HIRONAKA. Sensitivity of frequency plots for detecting vegetation change. 279-286
SMYTHE, S. R. *see* Hutchinson and Smythe, 36-41
Snowy Range, Wy
brook trout: Chisholm and Hubert, 137-139
soils
in Whatcom County, Wa: Goldin, 61-66
South Dakota
radiation from mill tailings: Rumble, 145-149
spruce
Engelmann (*Picea engelmannii*) seedling temperature tolerance: Seidel, 1-7
squawfish
northern (*Ptychocheilus oregonensis*) abundance: Kirn, Ledgerwood and Nelson, 197-200
STARKEY, R. G. *see* Fielder and Starkey, 186-190
stichaeoid fish
Anoplarchus purpurescens and *Pholis ornata*, food habits: Barton, 125-130
streams
discharge and timber management: Duncan, 258-264
SWANSON, S. R. *see* Doescher, Miller, Swanson and Winward, 55-60

TANK, S. L. and W. B. SIDLE. Habitat relationships of wintering passerines in the River of No Return Wilderness Area of central Idaho. 238-242
TAYLOR, R. J. *see* Shaw and Taylor, 21-31
trout
brook (*Salvelinus fontinalis*) in Wyoming: Chisholm and Hubert, 137-139
turkeys
Merriam's wild (*Meleagris gallopavo merriami*), brood habitat: Mackey, 108-112

uranium
mill tailings: Rumble, 145-149
URESK, D. W. *see* Sieg, Uresk and Hansen, 81-89, 218-224
Ursus *see* bears

VAVRA, M. *see* McInnis and Vavra, 265-270
vegetation change
detection by frequency plots: Smith, Bunting and Hironaka, 279-286
volcanoes
and chinook salmon: Kirn, Ledgerwood and Jensen, 191-196
and squawfish: Kirn, Ledgerwood and Nelson, 197-200
and zooplankton: Gaddy and Parker, 47-51
voles
western red-backed (*Clethrionomys californicus*) and mycophagy: Hayes, Cross and McIntire, 250-257

Washington
alpine plants and pollination: Shaw and Taylor, 21-31
ash and salmon diet: Kirn, Ledgerwood and Jensen, 191-196
bald eagle perch sites: Fielder and Starkey, 186-190
black and grizzly bears: Lyman, 67-72
geomorphology in Whatcom County: Goldin, 61-66
mountain goat census: Houston, Moorhead and Olson, 131-136
mycophagy in small mammals: Rhoades, 150-153
ruminants and selenium: Fielder, 15-20
sedimentary rocks of Manastash Formation: Lewellen, 160-165
sediments at Battle Ground Lake: Juvigné, 210-217
streams and timber management: Duncan, 258-264
wild turkey brood habitat: Mackey, 108-112
watersheds
streams and timber management, Duncan, 258-264
WINWARD, A. H. *see* Doescher, Miller, Swanson and Winward, 55-60
woodrats
ectoparasites of bushy-tailed (*Neotoma cinerea*) and dusky-footed (*N. fuscipes*): Cudmore, 174-178
Wyoming
brook trout: Chisholm and Hubert, 137-139

Yaquina Bay
stichaeoid fish: Barton, 125-130
YOUTIE, B. A. and R. F. MILLER. Insect predation on *Astragalus filipes* and *A. purshii* seeds. 42-46
zooplankton
and volcanic ash: Gaddy and Parker, 47-51

Reviewers of Manuscripts

The editor sincerely thanks the following persons who reviewed manuscripts for *Northwest Science* during the last year:

Dorald M. Allred
Kenneth M. Ames
Stephen F. Arno
M. B. Baker, Jr.
Joel Berger
Caroline Bledsoe
Jack D. Brotherson
Alan Busacca
William J. Cannon
Larry Carter
David L. Chance
Paul Claeyssens
Warren P. Clary
James L. Clayton
Roger del Moral
Charles H. Driver
Don E. Dumond
Lester E. Eberhardt
Alan W. Alcerman
George R. Fahnestock
Franklin F. Foit, Jr.
Richard P. Gale
E. O. Garton
David R. Gaylord
David L. Genter
Stanley P. Gessel
Gary E. Glass
Michael E. R. Godfrey
Don Goheen
Charles K. Graham
D. K. Grayson
Carl E. Gustafson
L. J. Heidmann
Thomas M. Hinckley
N. Thompson Hobbs
C. J. Hoffman
Peter R. Hooper
James Howard
Wayne A. Hubert
Donald R. Johnson
Barry L. Keller
Richard L. Knight
Earl J. Larrison
Gary Larson
James E. Lotan
William Lopushinsky
L. Jack Lyon
Richard N. Mack
Chris Maser
Dean E. Medin
Walter F. Megahan
Peter J. Mehringer, Jr.
P. L. Meserve
L. H. Metzgar
Maynard M. Miller
Sherman A. Minton
Michael Moody
Henry A. Pearson
David Perry
Kerry Paul Reese
W. J. Reitveld
James B. Reynolds
Timothy D. Reynolds
Mary F. Ricks
Charles T. Robbins
Frank Ronco, Jr.
Lewis F. Roth
Kenelm Russell
Susan Schwab
E. Lamar Smith
Joseph T. Springer
Douglas G. Sprugel
Fred Swanson
Kenneth Swedberg
Gary Thorgaard
Kristiina Vogt
Ronald H. Wakimoto
Richard L. Wallace
William Weaver
Bruce L. Welch
Neil E. West
Stephen D. West
John O. Whitaker, Jr.
Clinton K. Williams
David J. Wollkind
Donald B. Zobel

For *Northwest Science* and the other editors, I extend sincere thanks to Caroline Hooper for once again volunteering her services as a professional indexer to prepare the comprehensive index for volume 60 that appears in this issue.

Honorary Life Members

Ewart M. Baldwin
Irven O. Buss
L. C. Cady
Charles D. Campbell
Julian L. Culbertson
Rexford Daubenmire
Glenn Deitschman
R. A. Diettert
Bruce V. Ettling
William K. Ferrell
C. Clement French
Stanley P. Gessel
N. S. Golding
Phil Haddock
H. P. Hansen
Adolph Hecht
Kenneth Holmes
G. Brooks King
Rufus W. Kiser
Lewis and Clark High School Library (In memory of Thomas Large and J. G. McCracken)
Joseph W. Mills
Milton M. Mosher
Richard J. Naskali
Frank D. Nicol
Frances J. Schadegg
C. Gardner Shaw
Leona M. Sundquist
Robert F. Tarrant
Richard B. Walker
D. J. Wort

1986 Sustaining Institutional Members

Battelle Northwest, Richland, Washington
EG&G Idaho, Inc., Idaho Falls, Idaho
MacMillan Bloedel, Ltd., Nanaimo, British Columbia, Canada
Potlatch Corporation, Lewiston, Idaho
The Washington Water Power Company, Spokane, Washington
Weyerhaeuser Company, Centralia, Washington

1986 Institutional Members

Boise State University, Boise, Idaho
British Columbia Institute of Technology, Burnaby, British Columbia, Canada
Central Oregon Community College, Bend, Oregon
Central Washington University, Ellensburg, Washington
Centralia College, Centralia, Washington
College of Idaho, Caldwell, Idaho
Eastern Montana College, Billings, Montana
Eastern Oregon State College, LaGrande, Oregon
Eastern Washington University, Cheney, Washington
Edmonds Community College, Lynnwood, Washington
The Evergreen State College, Olympia, Washington
George Fox College, Newberg, Oregon
Grays Harbor College, Aberdeen, Washington
Green River Community College, Auburn, Washington
Highline Community College, Midway, Washington
Idaho State University, Pocatello, Idaho
Lewis-Clark State College, Lewiston, Idaho
Lewis and Clark College, Portland, Oregon
Linfield College, McMinnville, Oregon
Montana College of Mineral Science and Technology, Butte, Montana
Mt. Hood Community College, Gresham, Oregon
North Idaho College, Coeur d'Alene, Idaho
Northern Montana College, Havre, Montana
Pacific Lutheran University, Tacoma, Washington
Pacific University, Forest Grove, Oregon
Peninsula College, Port Angeles, Washington
Portland State University, Portland, Oregon
St. Martin's College, Lacey, Washington
Shoreline Community College, Seattle, Washington
Simon Fraser University, Burnaby, British Columbia, Canada
Skagit Valley College, Mount Vernon, Washington
Southern Oregon State College, Ashland, Oregon
Southwestern Oregon Community College, Coos Bay, Oregon
Spokane Falls Community College, Spokane, Washington
University of Alaska, Fairbanks, Alaska
University of Idaho, Moscow, Idaho
University of Montana, Missoula, Montana
University of Puget Sound, Tacoma, Washington
University of Victoria, British Columbia, Canada
University of Washington, Seattle, Washington
Walla Walla College, College Place, Washington
Washington State Library, Olympia, Washington
Washington State University, Pullman, Washington
Western Washington University, Bellingham, Washington
Whitman College, Walla Walla, Washington
Whitworth College, Spokane, Washington
Yakima Valley College, Yakima, Washington

1986 Sustaining Individual Members

Donald J. Brown, Richland, Washington
Randall E. Brown, Pasco, Washington
Nelsa M. Buckingham, Port Angeles, Washington
John H. Crow, Port Murray, New Jersey
Bruce Ettling, Vancouver, Washington
George R. Fahnestock, Seattle, Washington
William H. Funk, Pullman, Washington
Gerald H. Haddock, Wheaton, Illinois
Donald Hanley, Seattle, Washington
Charles R. Hatch, Moscow, Idaho
Mary M. Hektner, Arcata, California
Francis R. Herman, Fairbanks, Alaska
Richard K. Hermann, Corvallis, Oregon
Barry L. Keller, Pocatello, Idaho
Giles W. Maloof, Boise, Idaho
Emmett B. Moore, Jr., Richland, Washington
Howard R. Panik, Carson City, Nevada
William H. Rickard, Richland, Washington
Edward S. Schreiner, Port Angeles, Washington
Dale Stradling, Cheney, Washington
Robin J. Tausch, Reno, Nevada
Daniel W. Uresk, Rapid City, South Dakota
George H. Ward, Husum, Washington
Shepard M. Zedaker, Christiansburg, Virginia

Northwest Science

General Information

Publication in *Northwest Science* is open to scientists in the basic, applied, and social sciences who are engaged in original or fundamental research. *Northwest Science* does not publish notes, letters, or bibliographic papers. All submissions are reviewed by at least two referees and one associate editor. While submissions from outside the Pacific Northwest are welcome, at least one author of all papers considered for publication must be a member of the Northwest Scientific Association.

Information for Authors—A complete copy of the *Northwest Science* "Information for Authors" is available from the Editor.

Page Charges—Page charges are currently $60 per printed page. Petition for partial payment or waiver of these charges should be directed to the Editor upon the manuscript's being accepted for publication.

Manuscripts—Submit three copies of the paper (including tables and figures) to the Editor. Manuscripts should be typewritten on 8½x11 paper and *double-spaced throughout (including abstract, acknowledgments, literature cited, tables, and legends for figures);* provide ample margins. Avoid unnecessary footnotes. Do not break words at the end of a line. Format and style of manuscripts should conform to general usage in recent issues.

An abstract, written in complete sentences and not exceeding 250 words, should precede every article. It should succinctly state the objectives, the experimental design, the principal observations, and conclusions of the paper. Authors are reminded of the diverse disciplines and readership served by the journal; with this in mind, the abstract should conclude with a sentence or two stating the broader significance of the paper.

Literature citations should have the author's name and year of publication in the text; e.g. (Jones 1978). Citations should be double-spaced and listed in alphabetical order at the end of the article.

Present all data in international (SI) units. English equivalents may be added parenthetically. Use the 24-hour clock (0600 and 2300) and continental dating (17 November 1982).

Equations should be presented camera-ready. Symbols should be large enough to be legible after a ⅓ to ½ reduction in size, but not overly large.

Tables should be typewritten (double-spaced) separately from the text. Original art work or glossy prints of photographs must be submitted for reproduction. Art work and lettering should be large enough (but not overly large) to provide clarity after a 50 percent reduction in size for printing. The author's name and figure number should be penciled on the back of each illustration. Provide a scale for distance on map illustrations. Legends for illustrations should be typed (double-spaced) as a section of the manuscript; do not use a separate page for each legend.

Length of manuscripts is limited to 15 pages of printed copy. Two typed pages are approximately equal to one journal page.

Authors of Biological Papers—On first mention, a species should be designated by common name followed by systematic binomial. For abbreviations and forms of titles for serial publications, follow the *BIOSIS List of Serials.* Consult with the *Council of Biology Editors (CBE) Style Manual,* 4th ed., for general information on manuscript preparation.

Correspondence—Correspondence will be between senior author and the Editor.

Editing—In addition to being reviewed by two referees and an associate editor, manuscripts will be edited for grammatical correctness and clarity.

Galley Proofs and Reprints—One set of proofs will be sent to the senior author for correction shortly before publication; proofs should be returned to the Editor within three days of receipt. Senior authors should inform the Editor of any change of address for handling proofs. Reprints must be ordered when the proofs are returned. A schedule of reprint prices will be sent to the author with the proofs.

Non-Profit Org.
BULK RATE
U.S. POSTAGE
PAID
PULLMAN, WA
Permit No. 1

Northwest Science

Quarterly Publication of the Northwest Scientific Association

MR F N MacMILLAN NWS
WSU/HOLLAND LIBRARY
PULLMAN WA 99164-5610

Papers published in *Northwest Science* are indexed in *Current Contents, Science Citation Index, Biological Abstracts, The Zoological Record, Recent Literature Supplement to The Auk, Abstracts in Anthropology, Bibliography and Index of Geology, Chemical Abstracts, Bibliography of Agriculture, Forestry Abstracts,* and *University Microfilms.*

Northwest Science is offered in exchange to other colleges, universities, learned societies, and libraries. Publications sent in exchange should be addressed to Washington State University Library, Technical Services Division, Pullman, Washington 99164-5610, U.S.A.

8489

May 1987 Volume 61, Number 2

NORTHWEST SCIENCE

CONTENTS

65 Bison West of the Rocky Mountains: An Alternative Explanation—**Dirk Van Vuren**

70 Effects of Cattle Grazing Upon Chemical Constituents Within Important Forages for Elk—**W. J. Dragt and K. M. Havstad**

74 Slope Use by Cattle, Feral Horses, Deer, and Bighorn Sheep—**David Ganskopp and Martin Vavra**

82 Summer Birds of the Upper Subalpine Zone of Mount Adams, Mount Rainier, and Mount St. Helens, Washington—**David A. Manuwal, Mark H. Huff, Michael R. Bauer, Christopher B. Chappell, and Karen Hegstad**

93 Effects of Lowered Salinity on Activity of the Ghost Shrimp *Callianassa californiensis*—**Martin H. Posey**

97 Evaluation of Soil Nutrients, pH, and Organic Matter in Rangelands Dominated by Western Juniper—**Paul S. Doescher, Lee E. Eddleman and Milda R. Vaitkus**

103 Identification of *Phytophthora* spp. known to Attack Conifers in the Pacific Northwest—**P. B. Hamm and E. M. Hansen**

110 Stability of Venoms from the Northern Pacific Rattlesnake (*Crotalus viridis oreganus*)—**Edward K. Johnson**

114 Abundance, Foraging, and Roosting of Bald Eagles Wintering in the Harney Basin, Oregon—**Frank B. Isaacs and Robert G. Anthony**

122 The Distribution, Habitat and Population Characteristics of Fluvial Arctic Grayling (*Thymallus arcticus*) in Montana—**George A. Liknes and William R. Gould**

130 Poisonous Snakes and Snakebite in the U.S.: A Brief Review—**Sherman A. Minton**

Northwest Scientific Association

(Founded 1923)

The Northwest Scientific Association, an affiliate of the American Association for the Advancement of Science, is an association representative of the basic and applied sciences and of social sciences.

Membership in the Northwest Scientific Association, which includes a subscription to *Northwest Science,* is open to individuals in the Northwest (Washington, Idaho, Oregon, Western Montana, British Columbia), for $14 per year ($8 per year for students). Institutional memberships, $40 per year. All other individual subscribers $25 per year. Sustaining membership, $25 per year for individuals and $100 per year for organizations, institutions, or agencies. Subscriptions are for the calendar year only.

Send change of address, payment of dues, or requests for undelivered issues to the Treasurer.

Editor of *Northwest Science*

Kenneth V. Kardong
Department of Zoology
Washington State University
Pullman, Washington 99164-4220

Officers of the Association

President Steven D. Tesch*
Oregon State University
Corvallis, Oregon (1989)

President-Elect W. H. Rickard
Pacific Northwest Laboratory
Richland, Washington (1990)

Secretary George H. Fahnestock
Seattle, Washington (1990)

Treasurer Robert K. Moseley
The Nature Conservancy
1221 South Main Street
Moscow, Idaho 83843 (1989)

Past President Donald Hanley
Washington State University
c/o University of Washington
Seattle, Washington (1988)

Trustees:

Robert Antibus
University of Montana
Missoula, Montana (1988)

Steven Benham
Pacific Lutheran University
Tacoma, Washington (1988)

Dan L. Campbell
United States Dept. of Agriculture
Olympia, Washington (1990)

Robert L. Carr
Eastern Washington University
Cheney, Washington (1990)

Richard A. Cellarius
Evergreen State College
Olympia, Washington (1988)

Wilbert R. Danner
University of British Columbia
Vancouver, B.C. (1989)

Kenneth Hammond
Central Washington University
Ellensburg, Washington (1989)

David Hansen
Pacific Lutheran University
Tacoma, Washington (1990)

Larry Larson
Oregon State University
Corvallis, Oregon (1988)

William Lopushinsky
U.S. Forest Service
Wenatchee, Washington (1990)

Gilbert B. Pauley
University of Washington
Seattle, Washington (1989)

William R. Rayburn
Washington State University
Pullman, Washington (1989)

W. H. Rickard
Pacific Northwest Laboratory
Richland, Washington (1988)

Harry Smith
University of British Columbia
Vancouver, B.C. (1988)

Steven D. Tesch
Oregon State University
Corvallis, Oregon (1988)

David H. Wagner
University of Oregon
Eugene, Oregon (1989)

H. Clare Wiser
Washington State University
Pullman, Washington (1990)

*Term of office expires in the year given in parentheses.

May 1987 Volume 61, Number 2

NORTHWEST SCIENCE

Editor	Kenneth V. Kardong	Washington State University
Managing Editor	Fred Bohm	Washington State University
Associate Editors		
Aquatic Biology	Gary L. Larson	U.S. National Park Service/ Oregon State University
Botany	Suzanne M. Schwab	Eastern Washington University
Chemistry and Physics	Frank L. Curzon	University of British Columbia
Engineering and Mathematics	Gary L. Sheldon	Washington State University
Forestry	James K. Agee	U.S. National Park Service/ University of Washington
Geology	Franklin F. Foit, Jr.	Washington State University
Social Sciences	Philip D. Young	University of Oregon
Soils	Robert L. Edmonds	University of Washington
Wildlife Biology	Margaret A. O'Connell	Washington State University
Zoology	Kerry Paul Reese	University of Idaho

CONTENTS

65 Bison West of the Rocky Mountains: An Alternative Explanation—**Dirk Van Vuren**

70 Effects of Cattle Grazing Upon Chemical Constituents Within Important Forages for Elk—**W. J. Dragt and K. M. Havstad**

74 Slope Use by Cattle, Feral Horses, Deer, and Bighorn Sheep—**David Ganskopp and Martin Vavra**

82 Summer Birds of the Upper Subalpine Zone of Mount Adams, Mount Rainier, and Mount St. Helens, Washington—**David A. Manuwal, Mark H. Huff, Michael R. Bauer, Christopher B. Chappell, and Karen Hegstad**

93 Effects of Lowered Salinity on Activity of the Ghost Shrimp *Callianassa californiensis*—**Martin H. Posey**

97 Evaluation of Soil Nutrients, pH, and Organic Matter in Rangelands Dominated by Western Juniper—**Paul S. Doescher, Lee E. Eddleman and Milda R. Vaitkus**

103 Identification of *Phytophthora* spp. known to Attack Conifers in the Pacific Northwest—**P. B. Hamm and E. M. Hansen**

110 Stability of Venoms from the Northern Pacific Rattlesnake (*Crotalus viridis oreganus*)—**Edward K. Johnson**

114 Abundance, Foraging, and Roosting of Bald Eagles Wintering in the Harney Basin, Oregon—**Frank B. Isaacs and Robert G. Anthony**

122 The Distribution, Habitat and Population Characteristics of Fluvial Arctic Grayling (*Thymallus arcticus*) in Montana—**George A. Liknes and William R. Gould**

130 Poisonous Snakes and Snakebite in the U.S.: A Brief Review—**Sherman A. Minton**

Announcements

This issue revives from the early years of the journal a useful and successful type of feature, the review article. More are planned that touch upon other areas of interest served by *Northwest Science.* The article appearing at the end of this issue deals with snakebite. It was written by Dr. Sherman A. Minton. Throughout his professional career, Dr. Minton has published a wide variety of research papers in the area of toxicology with emphasis on just this subject, snakebite. Although presently retired from the faculty of Microbiology and Immunology at the Indiana University School of Medicine, he continues an active research interest in venomous reptiles.

My sincere thanks to Sherman Minton for preparing for us this review article that summarizes some of the most recent thinking upon the strategy of treatment of snakebite. I am pleased that *Northwest Science* can offer this special feature to our readership.

—Editor

Dirk Van Vuren, Department of Systematics and Ecology
University of Kansas, Lawrence, Kansas 66045

Bison West of the Rocky Mountains: An Alternative Explanation

Abstract

Although abundant on the Great Plains, bison (*Bison bison*) were relatively scarce west of the Rocky Mountains in the Pacific Northwest. Four explanations have been advanced to account for this low density: 1) relative inaccessibility of the area, coupled with Indian-caused mortality; 2) low protein content of forages; 3) lack of synchrony between forage plant phenology and the bison reproductive cycle; 4) periodically heavy winter snows deep enough to kill all colonizing bison. None of these explanations finds solid support in the available evidence. I propose that low bison numbers resulted from low overall forage production, and from discontinuous habitat which isolated bison populations and slowed recolonization following periodic local extinctions.

Introduction

The former distribution and extraordinary abundance of bison (*Bison bison*) on the Great Plains has been chronicled in detail (Roe 1970), but the occurrence of bison further west is not well known and has been a matter of considerable debate. Although bison apparently were widely distributed throughout much of the Pacific Northwest, they were abundant west of the Continental Divide only in southwestern Wyoming and southeastern Idaho. Low density of bison over most of their range west of the Divide stands in marked contrast to availability of steppe habitat which seemed capable of supporting much higher numbers. This disparity between numbers and apparent carrying capacity was noted by the earliest explorers in the area, and has stimulated much discussion since (Kingston 1932, Haines 1967, Christman 1971, Schroedl 1973, Butler 1978, Mack and Thompson 1982, Daubenmire 1985). Resolution of the problem has important implications for plant ecology and evolution (Daubenmire 1978, 210, Mack and Thompson 1982), zoogeography (Lyman and Livingston 1983), and ethnography (Schroedl 1973, Butler 1978).

Four explanations have been proposed to account for the scarcity of bison west of the Rocky Mountains. Critical evaluation of these explanations, based on available literature, has been lacking. Because the problem is historical in nature (bison were exterminated west of the Rocky Mountains over 100 years ago), the cause of low bison numbers may never be identified conclusively; yet a considerable body of pertinent literature exists, largely overlooked by previous authors. My purpose is to examine the four explanations in light of the available evidence, then propose a new explanation.

Former Distribution of Bison

Numerous eyewitness accounts attest to the abundance of bison in southwestern Wyoming and the Snake River Plain and adjacent valleys of southeastern Idaho (*e.g.,* Ogden 1910, Work 1913, Davis 1935, Haines 1955). There are no eyewitness accounts of bison further west and northwest, in the Pacific Northwest, but broad distribution is suggested by recovery of bison skulls and other bones from at least 44 localities in eastern Washington, eastern Oregon, and southwestern Idaho (hereafter "PNW") (Schroedl 1973, Agenbroad 1978, Van Vuren and Bray 1985). Only one of these localities yielded evidence of more than a few individuals; hundreds of bison skulls were exposed at Malheur Lake in eastern Oregon, suggesting that bison may have been locally common there (Van Vuren and Bray 1985). Most of the 44 localities were in areas characterized by steppe vegetation which produces an appreciable biomass of graminoids, the principal forage of bison (Meagher 1973, Peden 1976, Reynolds *et al.* 1978, Van Vuren 1984a). Available evidence suggests that bison became extinct for uncertain reasons in eastern Oregon and Washington about 1800 (Schroedl 1973, Van Vuren and Bray 1985).

Previous Explanations

Kingston (1932) argued that physiographic barriers greatly restricted immigration of bison into the PNW, and that the few successful immigrants

were soon killed by Indians. Archeological evidence does not support this explanation. The presence of bones of immature bison in archeological sites in southeastern Washington suggests that a breeding population inhabited the area (Osborne 1953, Schroedl 1973). A bison kill site in southwestern Idaho, in use an estimated 7000 years, incorporated 2680 m of stone fences (Agenbroad 1978); the effort for construction and the duration of use suggest that bison in the area were an established population rather than an occasional group that strayed west.

Johnson (1951), noting the apparently low densities of bison on tallgrass prairie east of the Mississippi River compared with high densities on shortgrass prairie further west, suggested that bison numbers were limited by presumed lower protein content of tallgrass species. Daubenmire (1985) interpreted this suggestion as an explanation of low bison numbers in the PNW as compared with high numbers on the Great Plains. Data on protein content of grasses do not support this interpretation. Protein content of steppe grasses in the PNW, either live (*ca.* 6-15% of dry weight) or cured (*ca.* 4-7%) (McIlvanie 1942, Rickard *et al.* 1975, Uresk and Cline 1976, Willms *et al.* 1981), was similar to protein content of live (*ca.* 6-15%) or cured (*ca.* 3-8%) steppe grasses east of the Rocky Mountains (Jefferies and Rice 1969, Sims *et al.* 1971, Willard and Schuster 1973, Goetz 1975, Cogswell and Kamstra 1976).

Mack and Thompson (1982) suggested that grass phenology in the PNW may have limited bison numbers. They noted that bison cows usually calve late April through early June and proposed that the nutritional stress of lactation coincided well with grass phenology on the Great Plains, but very poorly with phenology in the PNW, where steppe grasses are dormant during much of the summer. The underlying assumption, that the bison reproductive cycle cannot shift in response to forage availability, may not be valid. The midpoint of the breeding season of seven bison herds (McHugh 1958, Halloran and Glass 1959, Fuller 1962, Meagher 1973, Petersburg 1973, Mahan 1978, Lott 1981, Lott and Galland 1985, Shull 1985) was correlated with latitude ($R_s = 0.75$, $P < 0.05$). Breeding, and presumably calving, occurred up to six weeks earlier in southern herds than in northern herds, suggesting that the bison reproductive cycle can shift according to environmental conditions. Moreover, Daubenmire (1985) argued that grasses in more mesic habitats peripheral to steppe remain green throughout the summer, providing sufficient forage to sustain a substantial number of bison. The ability of bison to exploit seasonally available forage is demonstrated by the several extant herds which are migratory (Soper 1941, Meagher 1973, Van Vuren and Bray 1986).

Daubenmire (1985) proposed that occasionally heavy snowfall west of the Rocky Mountains, held in place by shrubs, was sufficiently deep to kill any bison that crossed the Continental Divide. Telfer and Kelsall (1984) reported that bison seemed less efficient than several other native North American ungulates at coping with deep snow, but it is unknown if this relative inefficiency translated into an absolute inability to survive in the PNW. There is a crucial difference between snowfall sufficient to cause local mortality in bison, which has been documented (Meagher 1973), and snowfall periodically so severe that a vast area was rendered entirely uninhabitable. Daubenmire derives support for his explanation largely from historical accounts of domestic livestock encountering difficulty with deep snow. The underlying assumption, that bison and livestock are ecologically similar, is probably invalid (e.g., Peden *et al.* 1974; Christopherson *et al.* 1978; Schwartz and Ellis 1981; Van Vuren 1982, 1984a; Van Vuren and Bray 1983). Moreover, there are numerous reliable descriptions from the 1800's of factors such as drowning, fire, and quicksand killing large numbers of bison, but none of mass mortality due to deep snow (Roe 1970). Indeed, historical accounts indicate bison were not greatly affected by snow (Roe 1970, 203).

Any explanation for low bison numbers in the PNW should also account for the disappearance of bison in the area about 1800. Christman (1971) suggested that this extinction, which occurred shortly after local Indians acquired the horse, resulted from the increased efficiency and mobility of mounted hunters. The preference of Indians for bison is demonstrated by numerous accounts of PNW tribes making trips of 500 km or more on horseback to hunt bison east of the Continental Divide (e.g., Ogden 1910, Stewart 1938). Daubenmire (1985), however, argued that Christman's suggestion was inconsistent with

Schroedl's (1973) conclusion that bison numbers in eastern Washington were seemingly in decline long before introduction of the horse. Schroedl's conclusion was based on a temporal decline in numbers of archeological sites in which bison have been found and in numbers of bison bone fragments per site. This evidence is questionable. The decline in number of sites containing bison, from nine (2500-1500 BP) to six (500-200 BP), is unconvincing. Schroedl did not compare the number of sites in which bison were found with the number in which they were not found; a higher number of older sites containing bison could simply reflect a higher number of such sites being excavated. The temporal decrease in bison bone fragments resulted entirely from the disproportionate influence of one of the 22 sites excavated; this site was among the oldest and contained 74% of all bison bone fragments recovered. Moreover, Butler (1978) noted that changes in number of bison bone fragments found in archeological sites could be more a reflection of changes in local hunting patterns than of trends in bison numbers. The data are inadequate for any conclusion about pre-extinction changes in bison numbers; hence, increased hunting efficiency of mounted Indians remains a valid explanation of extinction of bison in the PNW.

A New Explanation

I propose that low bison numbers in the PNW resulted from low carrying capacity and from periodic local extinctions followed by slow rates of recolonization. This theory hinges on two heretofore unconsidered differences in steppe vegetation and physiography east and west of the Rocky Mountains. First, production of herbaceous vegetation in steppe communities was much lower in the PNW than in the Great Plains. Herbaceous biomass production in ungrazed PNW steppes was *ca.* 400-1500 kg/ha (Daubenmire 1970, Rumsey 1971, Rickard 1985), compared with *ca.* 1500-3500 kg/ha or more in the Great Plains (Dix 1960, Hulett and Tomanek 1969, Shiflet and Dietz 1974). Densities of bison were lower west of the Rocky Mountains than east simply because of lower carrying capacity. Early dormancy of steppe vegetation may have further reduced carrying capacity (Mack and Thompson 1982).

Second, vegetation east of the Rocky Mountains consisted of nearly continuous grassland, virtually all of it suitable bison habitat. Any area suffering a local population reduction or extinction of bison could be recolonized quickly by adjacent herds. In contrast, much of the terrain west of the Rocky Mountains was a mosaic of habitats, many of them unsuitable for bison. Distribution of bison probably was disjunct, with physiographic barriers such as mountains, deserts, or deep canyons hindering movement of individuals between many populations. McDonald (1981, 227) found a high incidence of dental anomalies among bison skulls recovered from Malheur Lake and suggested they were from an isolated, inbred population. Dental anomalies have been associated with small initial size and potential inbreeding in other bison populations (Van Vuren 1984b). Periodically, deep snow (Daubenmire 1985), concerted hunting effort by pre-horse Indians (Kingston 1932), or other mortality factors may have caused local extinctions. Slow immigration rates probably left such areas vacant of bison for many years, serving to further reduce overall numbers in the PNW. The large number of bison skulls found at the bottom of Malheur Lake may represent a herd that mired in the mud during summer or broke through the ice during winter and drowned. Both events were important causes of mass mortality of bison on the Great Plains (Roe 1970).

Acquisition of the horse by Indians probably led to increased hunting mortality of bison; 1000 were killed by a band of Indians in southeastern Idaho in one day, without firearms (Haines 1955, 36). On the Great Plains, continuous, productive habitat permitted rapid recolonization by adjacent herds. In the PNW, however, low densities throughout the area and slow recolonization resulted in rapid extinction.

Acknowledgments

I thank K. B. Armitage, B. E. Coblentz, R. S. Hoffmann, and C. E. Martin for critically reviewing the manuscript.

Literature Cited

Agenbroad, L. D. 1978. Buffalo jump complexes in Owyhee County, Idaho. Plains Anthropol. 23(82):213-221.

Butler, B. R. 1978. Bison hunting in the desert west before 1800: the paleo-ecological potential and the archaeological reality. Plains Anthropol. 23(82):106-112.

Christman, G. M. 1971. The mountain bison. Am. West 8(3)44-47.

Christopherson, R. J., R. J. Hudson, and R. J. Richmond. 1978. Comparative winter bioenergetics of American bison, yak, Scottish Highland and Hereford calves. Acta Theriol. 23:49-54.

Cogswell, C., and L. D. Kamstra. 1976. The stage of maturity and its effect upon the chemical composition of four native range species. J. Range Manage. 29:460-463.

Daubenmire, R. F. 1970. Steppe Vegetation of Washington. Wash. Agric. Exp. Sta. Tech. Bull. 62. Washington State University.

_____. 1978. Plant Geography. Academic Press, New York.

_____. 1985. The western limits of the range of the American bison. Ecology 66:622-624.

Davis, W. B. 1935. Mammals of the Ross Expedition (1824) in Idaho. Murrelet 16:7-10.

Dix, R. L. 1960. The effects of burning on the mulch structure and species composition of grasslands in western North Dakota. Ecology 41:49-56.

Fuller, W. A. 1962. The Biology and Management of the Bison of Wood Buffalo National Park. Can. Wildl. Serv., Wildl. Manage. Bull. Ser. 1, No. 16.

Goetz, H. 1975. Effect of site and fertilization on protein content of native grasses. J. Range Manage. 28:380-385.

Haines, A. L. 1955. Osborne Russell's Journal of a Trapper. University of Nebraska Press, Lincoln.

Haines, F. 1967. Western limits of the buffalo range. Am. West 4(4):4-12, 66-67.

Halloran, A. F., and B. P. Glass. 1959. The carnivores and ungulates of the Wichita Mountains Wildlife Refuge, Oklahoma. J. Mammal. 40:360-370.

Hulett, G. K., and G. W. Tomanek. 1969. Forage production on a clay upland range site in western Kansas. J. Range Manage. 22:270-276.

Jefferies, N. W., and R. W. Rice. 1969. Nutritive value of clipped and grazed range forage samples. J. Range Manage. 22:192-195.

Johnson, C. W. 1951. Protein as a factor in the distribution of the American bison. Geogr. Rev. 41:330-331.

Kingston, C. S. 1932. Buffalo in the Pacific Northwest. Wash. Hist. Quart. 23:163-172.

Lott, D. F. 1981. Sexual behavior and intersexual strategies in American bison. Z. Tierpsychol. 56:97-114.

Lott, D. F., and J. C. Galland. 1985. Parturition in American bison: precocity and systematic variation in cow isolation. Z. Tierpsychol. 69:66-71.

Lyman, R. L., and S. D. Livingston. 1983. Late Quaternary mammalian zoogeography of eastern Washington. Quaternary Res. 20:360-373.

Mack, R. N., and J. N. Thompson. 1982. Evolution in steppe with few large, hoofed mammals. Am. Nat. 119:757-773.

Mahan, B. R. 1978. Aspects of American bison (*Bison bison*) social behavior at Fort Niobrara National Wildlife Refuge, Valentine, Nebraska, with special reference to calves. University of Nebraska, Lincoln. M.S. Thesis.

McDonald, J. N. 1981. North American Bison. University of California Press, Berkeley.

McHugh, T. 1958. Social behavior of the American buffalo (*Bison bison bison*). Zoologica 43:1-41.

McIlvanie, S. K. 1942. Carbohydrate and nitrogen trends in bluebunch wheatgrass, *Agropyron spicatum,* with special reference to grazing influences. Plant Physiol. 17:540-557.

Meagher, M. M. 1973. The Bison of Yellowstone National Park. Nat. Park Serv. Sci. Monogr. Ser., No. 1.

Ogden, P. S. 1910. Journal of Peter Skene Ogden; Snake Expedition, 1827-1828. Oregon Hist. Quart. 11:361-379.

Osborne, D. 1953. Archaeological occurrences of pronghorn antelope, bison, and horse in the Columbia Plateau. Sci. Monthly 77:260-269.

Peden, D. G. 1976. Botanical composition of bison diets on shortgrass plains. Am. Midl. Nat. 96:225-229.

Peden, D. G., G. M. Van Dyne, R. W. Rice, and R. M. Hansen. 1974. The trophic ecology of *Bison bison* L. on shortgrass plains. J. Appl. Ecol. 11:489-497.

Petersburg, S. J. 1973. Bull bison behavior at Wind Cave National Park. Iowa State University, Ames. M. S. Thesis.

Reynolds, H. W., R. M. Hansen, and D. G. Peden. 1978. Diets of the Slave River lowland bison herd, Northwest Territories, Canada. J. Wildl. Manage. 42:581-590.

Rickard, W. H. 1985. Experimental cattle grazing in a relatively undisturbed shrubsteppe community. Northw. Sci. 59:66-72.

Rickard, W. H., D. W. Uresk, and J. F. Cline. 1975. Impact of cattle grazing on three perennial grasses in south-central Washington. J. Range Manage. 28:108-112.

Roe, F. G. 1970. The North American Buffalo. 2nd. Edition. University of Toronto Press, Toronto.

Rumsey, W. B. 1971. Range seedings versus climax vegetation on three sites in Idaho. J. Range Manage. 24:447-450.

Schroedl, G. F. 1973. The Archaeological Occurrence of Bison in the Southern Plateau. Lab. Anthropol. Rep. Invest. No. 51. Washington State University.

Schwartz, C. C., and J. E. Ellis. 1981. Feeding ecology and niche separation in some native and domestic ungulates on the shortgrass prairie. J. Appl. Ecol 18:343-353.

Shiflet, T. N., and H. E. Dietz. 1974. Relationship between precipitation and annual rangeland herbage production in southeastern Kansas. J. Range Manage. 27:272-276.

Shull, A. M. 1985. Age-specific reproductive behavior of male American bison. Oklahoma State University, Stillwater. M.S. Thesis.

Sims, P. L., G. R. Lovell, and D. F. Hervey. 1971. Seasonal trends in herbage and nutrient production of important sandhill grasses. J. Range Manage. 24:55-59.

Soper, J. D. 1941. History, range and home life of the northern bison. Ecol. Monogr. 11:347-412.

Stewart, J. H. 1938. Basin-Plateau Aboriginal Sociopolitical Groups. Smithsonian Inst. Bur. Am. Ethnol. Bull. 120.

Telfer, E. S., and J. P. Kelsall. 1984. Adaptation of some large North American mammals for survival in snow. Ecology 65:1828-1834.

Uresk, D. W., and J. F. Cline. 1976. Mineral composition of three perennial grasses in a shrub-steppe community in south-central Washington. J. Range Manage. 29:255-256.

Van Vuren, D. 1982. Comparative ecology of bison and cattle in the Henry Mountains, Utah. *In* J. M. Peek and P. D. Dalke (eds.) Proc. Wildlife-Livestock Relationships Symp., For., Wildl., and Range Exp. Sta., University of Idaho, Moscow. Pp. 449-457.

_____. 1984a. Summer diets of bison and cattle in southern Utah. J. Range Manage. 37:260-261.

_____. 1984b. Abnormal dentition in the American bison, *Bison bison.* Can. Field-Nat. 98:366-367.

Van Vuren, D., and M. P. Bray. 1983. Diets of bison and cattle on a seeded range in southern Utah. J. Range Manage. 36:499-500.

_____. 1985. The Recent geographic distribution of *Bison bison* in Oregon. Murrelet 66:56-58.

_____. 1986. Population dynamics of bison in the Henry Mountains, Utah. J. Mammal. 67:503-511.

Willard, E. E., and J. L. Schuster. 1973. Chemical composition of six southern Great Plains grasses as related to season and precipitation. J. Range Manage. 26:37-38.

Willms, W., A. W. Bailey, A. McLean, and C. Kalnin. 1981. Effects of fall clipping or burning on the distribution of chemical constituents in bluebunch wheatgrass in spring. J. Range Manage. 34:267-269.

Work, J. 1913. Journal of John Work's Snake Country Expedition of 1830-31. Oregon Hist. Quart. 14:280-314.

Received 24 October 1986
Accepted for publication 12 January 1987

W. J. Dragt and **K. M. Havstad,** Department of Animal and Range Sciences
Montana State University, Bozeman, Montana 59717

Effects of Cattle Grazing Upon Chemical Constituents Within Important Forages for Elk[1]

Abstract

On many western rangelands, cattle and elk use the same forages but during different seasons. This can place these species into indirect competition or amensalism. The objective of this study was to examine the effects of summer grazing by cattle upon the winter forage quality for elk. Individual plants of bluebunch wheatgrass (*Agropyron spicatum*), rough fescue (*Festuca scabrella*), and Idaho fescue (*Festuca idahoensis*) were monitored for phenological stage when summer grazed by cattle on a Rocky Mountain elk (*Cervus elaphus nelsoni*) wintering range in the Elkhorn Mountains, Montana. Assessment of winter chemical composition of these three key forage species indicated no deleterious effects of summer grazing by cattle stocked at 3.7 ha/AUM upon the winter forage quality. In general, rough fescue and Idaho fescue had lower average fiber fractions and higher crude protein than bluebunch wheatgrass. Under deferred rotation cattle management, the primary winter elk forage management concern appears to be forage quantity rather than quality.

Introduction

In the Elkhorn Mountains of west-central Montana, up to 62% of elk winter diets was composed of Idaho fescue (*Festuca idahoensis*), rough fescue (*Festuca scabrella*) and bluebunch wheatgrass (*Agropyron spicatum*), the most abundant bunchgrasses on the winter range (DeSimone *et al.* pers. comm.). Other studies from Montana also reported that these three caespitose species comprise 50 to 90% of elk winter and spring diets (Gordon 1968, Stevens 1965).

Dietary components of cattle grazing summer ranges in the Pacific Northwest indicate similar reliance on these dominant bunchgrasses as key forage species (Holechek *et al.* 1982). Apparently use by cattle and elk of the same forages and nutrient supply at different times may create situations of indirect competition or amensalism. Although questions of dietary overlap have been addressed concerning these two species (Hansen and Reid 1975), this assessment has not been directed toward individual plants and the effect of grazing upon the resulting forage quality of the grazed plant.

The objective of this study was to quantify the effects of summer cattle grazing at various phenological stages of three key forage species upon resulting winter forage quality for elk.

Study Area and Methods

The study site was within the Muddy Lake and Jenkin's Gulch drainages, tributaries of Crow Creek located on the southeastern end of the Elkhorn Mountains in the Helena National Forest, Montana. This area comprises the South Crow cattle allotment, a rolling grassland with steep conifer filled draws and broader cottonwood dominated bottoms. Slopes and ridge tops have stony, loamy soils. Vegetation on the upland sites is dominated by bunchgrasses. Idaho fescue is nearly ubiquitous. Rough fescue occurs on slightly moister sites and bluebunch wheatgrass on most drier sites. The climate in the region is modified continental with large annual and daily temperature variations (DiSimone *et al.* pers. comm.). Elevation and annual precipitation range from 1464 m to 2100 m and 51 cm to 76 cm, respectively.

Approximately 200 elk have wintered in the study area since the 1960s (DeSimone *et al.* pers. comm.). Generally the area is used by elk from December to June. The South Crow cattle allotment (9300 ha) has been grazed with a three pasture, deferred rotation, grazing system since 1970. There are approximately 2500 animal unit months (AUM) allocated to 600 cows with calves (Anonymous USDA-Forest Service rep.). In 1983 the cattle grazing season was June 10 to October 15.

Defoliation responses of individual plants were quantified using permanent 10 m line transects marked by fixed end points (Gammon and Roberts 1978). Twenty-four transects were established on the study area with transects in five groups with three to six transects per group. Each group was subjectively located to include the three major forage plants and evidence of both

elk and cattle use. An average of six bluebunch wheatgrass plants, twenty-three Idaho fescue plants, and six rough fescue plants were contained within each transect. Line intercept of plant canopy determined inclusion of a plant in the sample population.

Transects were established in the spring, 1983, and sampled biweekly from June through October. Phenological stage and evidence of utilization of the three grass species were recorded. Eight phenological stages were identified: vegetative, boot (swelling visible in sheath to seedhead 50% out of the sheath), emerging seedheads (seedheads greater than 50% out of the sheath to fully emerged, but not filling), anthesis (any visible anthers regardless of condition), mature flowers (from seedheads filling to fully developed), seed shatter (any indication of disarticulation), mature foliage (seedheads completely empty and leaves dull green through brown), and fall regrowth (any new vegetative growth). Mature foliage was the overwintering stage. During March, 1984, all plants along the transects with known utilization histories from the previous summer were collected by removing the entire aboveground biomass from the sample population. Only plants which had been utilized once during the previous summer or were ungrazed were used for chemical analyses. Repeated defoliation of an individual plant was rarely observed.

Plant nitrogen and fiber related fractions were selected as the most useful for reflecting forage quality. Twenty percent of the individually-collected samples were randomly selected for chemical analyses using the AOAC (1980) procedures for crude protein (CP) and ash (ASH) and the procedures of Goering and Van Soest (1970) for neutral detergent fiber (NDF), acid detergent fiber (ADF) and acid detergent lignin (ADL). The remaining 80% of the samples were analyzed for CP, ASH, NDF, ADF and ADL by near-infrared spectrophotometry (NIR) as outlined by Norris *et al.* (1976) and Schenk *et al.* (1981). NIR calibration was achieved using the wet chemistry data obtained from 20% of the samples collected. Additionally, cellulose (CELL) and hemicellulose (HC) content was calculated as CELL = ADF − ADL and HC = NDF − ADF (Goering and Van Soest 1970). Analysis of variance was used to compare chemical constituent data between plant species and phenological stage when summer grazing had occurred. For constituents with significant F-values, the species means were separated using Least Significant Differences.

Results and Discussion

The phenological stage when either rough fescue or bluebunch wheatgrass had been grazed by cattle did not affect ($P > .05$) winter chemical composition (Table 1). Furthermore, grazed and ungrazed plants could not be distinguished by chemical analyses. For Idaho fescue, only NDF and ADF fiber fractions exhibited a response to the phenological stage when grazing occurred (Table 1). When grazed at seed shatter stage, Idaho fescue exhibited a reduction ($P < .05$) in both winter NDF and ADF contents compared to ungrazed plants and plants grazed during the vegetative or boot stages. Since other chemical constituents did not respond to summer grazing, these reductions in NDF and ADF percentages would not indicate a significant alteration of the winter forage quality of Idaho fescue.

An insufficient number of plants of each species were grazed during either the anthesis or mature flowers phenological stages to provide adequate samples for chemical analyses. Possible explanations for the absence of a negative response in forage quality to summer grazing include a single defoliation event for sampled plants, late spring defoliation as the earliest grazing event, and minimal tissue removal when summer grazed. All three explanations are probably correct to a degree.

McLean and Wikeem (1985a) indicated that injury to bluebunch wheatgrass was minimized when defoliation was either terminated early in the growing season allowing replenishment of depleted carbohydrate reserves, was infrequent, or avoided significant meristimatic tissue. Similar observations were reported for rough fescue (McLean and Wikeem 1985b). In the Elkhorns cattle grazing was not initiated until mid-June and defoliation would have occurred only after the vulnerable early spring vegetative stage. The deferred rotation livestock grazing system and light cattle stocking rate (approximately 3.7 ha/AUM) would also minimize both defoliation events and meristimatic tissue removal.

Mean values of winter chemical composition across all phenological stages demonstrated

TABLE 1. Winter (1984) chemical composition,[1] reported as percentage dry weight, of bluebunch wheatgrass (AGSP), Idaho fescue (FEID), and rough fescue (FESC) in relation to phenological stage when grazed, summer, 1983. Means in the same row followed by the same letter do not differ significantly ($P > .05$).

	PHENOLOGICAL STAGE						
	Vegetative	Boot	Seedheads Emerging	Seed Shatter	Mature Foliage	Fall Regrowth	Ungrazed
AGSP							
CP	5.1	3.6	3.6	4.0	3.4	NA	2.7
NDF	79.4	78.8	83.4	81.7	81.5	NA	82.4
ADF	50.3	53.2	57.3	53.8	53.9	NA	54.4
ADL	4.3	5.2	6.0	5.8	5.5	NA	5.5
CELL	46.0	48.0	51.3	48.0	48.4	NA	48.5
HC	29.1	25.6	26.1	27.9	27.6	NA	28.0
ASH	8.3	7.0	7.4	7.5	7.5	NA	7.3
FEID							
CP	6.0	5.4	5.8	6.2	6.5	6.0	6.2
NDF	77.8^{b}	76.1^{b}	71.8^{ab}	66.3^{a}	73.2^{ab}	72.4^{ab}	76.8^{b}
ADF	46.8^{b}	47.5^{b}	46.0^{b}	38.4^{a}	46.7^{b}	43.2^{ab}	46.2^{b}
ADL	3.7	3.6	3.7	5.7	4.6	3.8	4.4
CELL	43.1	43.9	42.3	32.7	42.1	39.4	41.8
HC	31.0	28.6	25.8	27.9	26.5	29.2	30.6
ASH	10.2	6.5	8.2	7.9	7.6	8.0	8.6
FESC							
CP	5.4	4.0	3.9	5.0	4.8	4.0	5.0
NDF	75.1	79.1	80.1	78.8	79.3	82.0	77.5
ADF	47.9	46.8	49.6	49.7	49.6	49.4	48.7
ADL	2.6	3.6	3.5	3.4	3.6	3.9	2.7
CELL	45.3	43.2	46.1	46.3	46.0	45.5	46.0
HC	27.2	32.3	30.5	29.1	29.7	32.6	28.8
ASH	8.4	6.2	7.0	10.0	8.8	7.4	8.2

[1]CP = crude protein, NDF = neutral detergent fiber, ADF = acid detergent fiber, ADL = acid detergent lignin, CELL = cellulose, HC = hemicellulose, and ASH = ash.

species differences (Table 2). Bluebunch wheatgrass, reported as the least preferred by elk of these three species (Gordon 1968), represented a typical dormant winter grass with low CP and high ADF and ADL composition. Nowak and Caldwell (1984) have reported winter photosynthetic activity by bluebunch wheatgrass in a cold steppe environment but that activity was minimal and was substantially reduced by cold temperature. The absence of fall regrowth by this species (Table 1) is not unusual (Quinton *et al.* 1982).

The lack of succulent leaf tissue and resulting lower preference by elk were reflected in the winter chemical composition. Bluebunch wheatgrass had the lowest ($P < .05$) average CP content in this study. Its CP content was below the generally accepted minimum of 5-6% required for rumen microbial function (Robbins *et al.* 1975).

Rough fescue, the most preferred grass on the South Crow winter range (Gordon 1968), had the lowest lignin values of the three forage species.

TABLE 2. Mean winter (1984) values for chemical constituent fractions as a percentage of dry weight for bluebunch wheatgrass (AGSP), Idaho fescue (FEID) and rough fescue (FESC). Means in the same row followed by the same letter do not differ significantly ($P > .05$).

CHEMICAL CONSTITUENT[1]	SPECIES		
	AGSP	FEID	FESC
CP	4^{c}	6^{a}	5^{b}
NDF	81^{a}	74^{b}	79^{a}
ADF	54^{a}	45^{c}	49^{b}
ADL	5^{a}	4^{b}	3^{c}
CELL	49^{a}	41^{c}	46^{b}
HC	27^{a}	29^{a}	30^{a}
ASH	7^{a}	8^{a}	8^{a}

[1]CP = crude protein, NDF = neutral detergent fiber, ADF = acid detergent fiber, ADL = acid detergent lignin, CELL = cellulose, HC = hemicellulose, and ASH = ash.

Low lignin values and intermediate levels of CP and other fiber constituents indicated some level of winter photosynthetic activity. Fall floral primordia initiation and slow winter development have been reported in rough fescue (Johnston and McDonald 1967).

Idaho fescue was apparently physiologically active through the winter. Fall initiation of floral primordia has also been reported in Idaho fescue (Johnston and McDonald 1967), and study site plants were observed with many greenish winter leaves. Winter CP content was similar to reported midsummer values (McCall 1939). An explanation for relatively lower structural carbohydrates (reflected in the CELL content) during the winter is that more easily metabolized carbohydrates are used in maintenance level respiration. Winter photosynthetic activity would provide some highly available carbohydrates, reducing tissue catabolism and preventing increased concentrations of CELL and ADL in the winter fiber component. For both fescues the apparent winter photosynthetic activity would generate greater tissue succulence contributing to the observed higher winter preference by elk (Gordon 1968) for these caespitose species.

Smith (1977) suggested that livestock grazing is the major factor restricting western wildlife production. Though management concerns surrounding dual use of rangelands by cattle and elk extend beyond questions of forage utilization, a key consideration is the impact one grazing species has on the forage quality available to the other. Operating primarily as grazers, cattle and elk in the northern Rockies extensively utilize caespitose grasses, especially wheatgrasses and fescues, though often during different seasons. In the Elkhorn mountains of west-central Montana cattle grazing is principally under the administration of the U.S. Forest Service and livestock rotation grazing systems are normally utilized. Within this setting it was observed that one summer cattle grazing event had no harmful effects upon the forage quality of the main key species of elk winter range. This observation would imply that under the current, deferred rotation grazing system, the primary consideration for winter forage allocation would be the quantity of available forage rather than its quality.

Notes

1. This research was a cooperative effort and jointly supported by the U.S. Forest Service Intermountain Research Station and the Montana Agricultural Experiment Station. Journal Paper No. J-1769.

Literature Cited

AOAC. 1980. Official methods of analysis (13th Ed.). Association of Official Analytical Chemists, Washington, D.C.

Gammon, D. M., and B. R. Roberts. 1978. Patterns of defoliation during continuous and rotational grazing of the Matopos Sandveld of Rhodesia. Rhod. J. Agr. Res. 16:117-131.

Goering, H. K., and P. J. Van Soest. 1970. Forage fiber analysis. ARS-USDA Agr. Handbook No. 379.

Gordon, F. A. 1968. Range relationships of elk and cattle on elk winter range, Crow Creek, Montana. Montana State University, Bozeman. Thesis.

Hansen, R. M., and T. D. Reid. 1975. Diet overlap of deer, elk, and cattle in southern Colorado. J. Range Manage. 28:43-47.

Holechek, J. L., M. Vavra, J. Skovlin, and W. C. Krueger. 1982. Cattle diets in the Blue Mountains of Oregon. II. Forests. J. Range Manage. 35:239-242.

Johnston, A., and M. D. McDonald. 1967. Floral initiation and seed production in *Festuca scabrella* Torr. Can. J. Plant Sci. 47:577-583.

McCall, R. 1939. Seasonal variation in the composition of bluebunch fescue. J. Agr. Res. 58:603-616.

McLean, A., and S. Wikeem. 1985a. Influence of season and intensity of defoliation on bluebunch wheatgrass survival and vigor in southern British Columbia. J. Range Manage. 38:21-26.

_____. 1985b. Rough fescue response to season and intensity of defoliation. J. Range Manage. 38:100-103.

Norris, K. H., R. F. Barnes, J. E. Moore, and J. S. Shenk. 1976. Predicting forage quality by infrared reflectance spectroscopy. J. Anim. Sci. 43:889-897.

Nowak, R. S., and M. M. Caldwell. 1984. Photosynthetic activity and survival of foliage during winter for two bunchgrass species in a cold-winter steppe environment. Photosynthetica 18:192-200.

Quinton, D. A., A. McLean, and D. G. Stout. 1982. Vegetative and reproductive growth of bluebunch wheatgrass in interior British Columbia. J. Range Manage. 35:46-51.

Robbins, C. T., P. J. Van Soest, W. W. Mautz, and A. N. Moen. 1975. Feed analyses and digestion with reference to whitetailed deer. J. Wildl. Manage. 39:67-79.

Schenk, J. S., I. Landa, M. R. Hoover, and M. O. Westerhaus. 1981. Description and evaluation of a near infrared reflectance spectrocomputer for forage and grain analysis. Crop Sci. 21:355-358.

Smith, R. J. 1977. Conclusions. *In* J. E. Townsend and R. J. Smith (eds.) Proc. of a Seminar on Improving Fish and Wildlife Benefits in Range Management. U.S. Fish and Wildl. Ser. Biol. Ser. Prog. FWS/OBS-77/1. Pp. 117-118.

Stevens, D. R. 1965. Range relationships of elk and livestock in the Crow Creek drainage, Elkhorn Mountains, Montana. Montana State University, Bozeman. Thesis.

Received 6 October 1986
Accepted for publication 18 December 1986

David Ganskopp, United States Department of Agriculture-Agricultural Research Service
Eastern Oregon Agricultural Research Center[1]
Star Rt. 1 4.51 Hwy. 205, Burns, Oregon 97720

and

Martin Vavra, Oregon State University, Eastern Oregon Agricultural Research Center
Star Rt. 1 4.51 Hwy. 205, Burns, Oregon 97720

Slope Use by Cattle, Feral Horses, Deer, and Bighorn Sheep[2]

Abstract

Patterns of slope utilization by cattle (*Bos* spp.), feral horses (*Equus caballus*), Rocky Mountain mule deer (*Odocoileus hemionus hemionus*), and California bighorn sheep (*Ovis canadensis californiana*) were monitored to compare their distributions to the topographic compositions of their respective habitats. The hypothesis that each species utilized slope classes in proportion to the topographic compositions of their respective habitats was rejected ($P < 0.01$). Bighorn sheep activities were not impaired by slopes of up to 80%. Cattle, horses, and deer demonstrated negative curvilinear responses to increasing slope with initial site avoidance exhibited on 20, 30, and 40% slopes, respectively. Where large expanses of level topography were available, cattle and horses made less use of steep slopes than their counterparts inhabiting more rugged terrain. These data demonstrate that cattle, horses, and deer should not be expected to make random use of forage resources in rugged terrain.

Introduction

An awareness of the distribution and movement patterns of large herbivores is particularly valuable to managers charged with allocating resources or assessing the impacts of utilization by large herbivores. The arrangement of food, water, and shelter, and their concurrent interactions with topographic features obviously influences the distribution of animals and their simultaneous use of an area's resources. Slope gradient may also be a major determinant of herbivore distribution in rugged terrain. With the exception of cattle (*Bos* spp.), few data are available describing the upper limits of slope use by large herbivores.

Cattle favor the relatively level ground associated with drainages, basins, and ridgetops (Glendening 1944, Blood 1961, Demarchi 1965, Julander and Jeffery 1964, Mueggler 1965, Phillips 1965, Cook 1966, Mackie 1970, Patton 1971, Gillen 1982, Barrett 1982). In general cattle limit their use of hillsides when grades approach 30% (Blood 1961, Patton 1971, Gillen 1982, Van Vuren 1982). Upslope presence of palatable forage (Gonzalez 1964, Cook 1966, Bryant 1982), salt (Champline and Talbot 1926, Skovlin 1965), or water (Skovlin 1965), however, may encourage additional utilization of hillsides.

Feral horses (*Equus caballus*) have an affinity for ridgetops or elevated terrain (Pellegrini 1971, Welsh 1975, Miller 1980, Keiper and Berger 1982); however, no one has attempted to quantify their use of hillsides. Pellegrini (1971) noted horses avoided steep hills, and that they rapidly traveled over unavoidable rough terrain.

Most workers report mule deer (*Odocoileus hemionus hemionus*) show little response to topographic variation (Demarchi 1965, Mackie 1970, Barrett 1982). Some observers report, however, that slope indirectly affects distribution of deer through its impact on snow accumulation and persistence (Wilkins 1957, Loveless 1967, Gilbert *et al.* 1970, Dusek 1975) or microclimate and vegetation patterns (Julander 1966, Loveless 1967, Mackie 1970).

Although bighorn sheep (*Ovis canadensis*) habitat is synonymous with rugged cliffs and highly dissected terrain (McCann 1953, Harris 1956, Russo 1956, McCullough and Schneegas 1966, Todd 1972, Jones 1980), few workers have addressed their use of rugged topography. Demarchi (1965) reported a positive correlation between the frequency of sightings of bighorn and increasing degree of slope, but provided no

[1]The Eastern Oregon Agricultural Research Center, including the Squaw Butte and Union Stations, is jointly operated by Oregon Agricultural Experiment Station and U.S. Department of Agriculture, Agricultural Research Service.

[2]This research was a cooperative effort jointly funded by the Bureau of Land Management, contract number YA-512-CT8-137, and the Eastern Oregon Agricultural Research Center. Technical paper number 7793. Oregon Agricultural Experiment Station.

information on the topographic composition of the study area. Shannon *et al.* (1975) found bighorn were neutral or may have discriminated against slope. They suggested the use of slopes was related to associated abiotic or biotic features rather than to slope per se.

In this project we monitored the frequency of use of slopes by cattle, feral horses, Rocky Mountain mule deer, and California bighorn sheep (*Ovis canadensis californiana*) from April 1979 through March 1981. Our goal was to establish thresholds of slope use for horses, deer, and bighorn sheep, and to supplement the information available for cattle. We first tested the hypothesis that each herbivore utilized slope classes in proportion to their availability. When this hypothesis was rejected, we further examined the data to detemine which slopes were favored or avoided.

Study Area

The study was conducted approximately 65 km south of Vale, Oregon, on a 375 km² area administered by the Bureau of Land Management. The area included three designated pastures, of roughly 62, 31, and 219 km², and an adjoining 63 km² unit to the south which contained a portion of the bighorn sheep range. Pasture boundaries consisted of 4-wire stock fencing, the east shoreline of the Owyhee Reservoir, and some natural barriers. Approximately 73% of the study area was within 1600 m of permanent water sources.

Topography ranged from well-eroded, gently-rolling hills to mountainous ridges, cliff rock, and canyons. Elevations ranged from 809 m, pool level of Owyhee Reservoir, to 1687 m. Major plant communities supported overstories dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) or low sagebrush (*Artemisia arbuscula*). Herbaceous layer dominants included bluebunch wheatgrass (*Agropyron spicatum*), Sandberg's bluegrass (*Poa sandbergii*), and cheatgrass (*Bromus tectorum*).

Historic overgrazing by large numbers of horses (up to 2500 in the 1940's), long-term seasonal use by livestock, and occasional wildfires have affected the distribution of plant communities on the area. Bluebunch wheatgrass, a large and palatable perennial bunchgrass, was most prevalent on slopes in excess of 20%. Cheatgrass and Sandberg's bluegrass, two species typically characterizing abused rangelands, were dominants in drainages and large basins where slopes were generally less than 20%. Wyoming big sagebrush and low sagebrush did not exhibit any systematic patterns of distribution. Detailed maps and descriptions of major plant communities are provided by Ganskopp (1984).

Feral horses and bighorn sheep were year-round residents. The total number of horses in the three pastures increased from 133 to 168 during our study. Bighorn sheep occupied a small portion of the largest pasture and the adjoining 63 km² area to the south. The herd consisted of about 100 animals.

Deer and cattle were seasonal occupants of the area. Approximately 200 to 300 deer wintered on the area from October through April. Cattle grazed the three pastures from April through October on a deferred rotation basis during both years of study. Their use totaled 1600 AUMs in 1979 and 3900 AUMs in 1980. Mean livestock density for the three pastures was 0.75 cows/km² in 1979 and 1.8 cows/km² in 1980.

Methods

The last two weeks of each month were devoted to surveying the study area in an attempt to plot the location of as many animals as possible. Binoculars and a 20 to 40X spotting scope facilitated long-range searching for large herbivores. Movement about the area was accomplished with four-wheel drive vehicles and by foot. Incidental sightings were also recorded and only animals initially unaware of our presence were utilized as data sources. We did not knowingly record duplicate observations of a recognized group or individual within a 24-hour period.

Percent slope of observation sites was measured with a clinometer. If more than one animal was involved, the measurement was made on an area deemed representative of the group. Each sighting was treated as a single observation, regardless of the number of animals involved. A coordinate grid, superimposed on a 1:63360 map of the study area, allowed documentation of sighting locations.

Because horses and bighorn sheep were year-round residents of the area, their data reflect a relatively uniform distribution of observations

over the two-year period. The only exception occurred in January, 1981, when three weeks of continuous fog hindered our searches for bighorn sheep. Our data for cattle and deer are strictly seasonal. Cattle were herded to the area in April and removed in late October each year. A few deer were continuously on the area, but their presence was most pronounced between October and April. Eighty-nine percent of our observations of deer were made during this period.

Visual examination of maps depicting sighting locations of the four herbivores revealed that cattle, horses, and bighorn sheep were either confined to, or chose to occupy only certain portions of the study area. Sightings of mule deer were well dispersed over the entire study area. Based on these distribution patterns, we defined the geographic boundaries of each herbivore's habitat. Consequently, our data depict only the habitat characteristics of areas frequented by each species.

Because cattle respected the fences and natural boundaries of the pastures, we assumed they occupied three distinct habitats on the area. Data were tallied by pasture with the assumption that an entire pasture was available for their use.

Horses on the area were easily identified by referencing sketches of distinguishing characteristics. Mean home range size (minimum convex polygon) was 12 km^2 with no seasonal shifts in home ranges occurring (Ganskopp and Vavra 1986). Six distinct herds of horses were identified during the study. Because bands and bachelors composing each herd appeared to restrict their movements voluntarily, we outlined the outermost coordinates of each herd with a minimum convex polygon (Southwood 1966), and assumed the circumscribed area constituted the available habitat of each herd. Three small herds (each supporting < 15 animals) were not included in this analysis.

Deer were observed throughout the study area. Total number of deer sighted was 1467 with 1157 animals classified to sex and age. Buck to doe ratios averaged 13.5/100, and fawn to doe ratios averaged 71.4/100. Because individual deer could not be identified or linked to a specific unit of land, we assumed the entire area was available for their use.

Bighorn sheep occupied a relatively restricted area in the more rugged southern portion of the study area. A minimum convex polygon, circumscribing 73 km^2, was used to define their habitat. Bighorn could be found at any location or elevation within their range throughout the duration of the study. Total number of bighorn sighted was 811 with 691 animals classified to sex and age. The lamb to ewe ratio averaged 54.1/100, and the ram to ewe ratio averaged 59/100.

Outlines of the study area and the various habitats were transferred to U.S. Geological Survey topographic maps. Map scale was 1:24000 with 12.19 m between contour intervals. A sample of 1545 randomly selected points were described to derive the topographic composition of the habitats. Distance between adjacent contour lines bracketing each point was measured and converted to horizontal distance. The vertical distance between contour intervals was divided by the horizontal distance between contour lines and multiplied by 100 to yield percent slope.

Data were compiled for each herbivore and habitat in 10% intervals ranging from 0 to 80+ % slope. Chi square analysis of homogeneity ($P < 0.05$) was used to test the null hypothesis (H_0) that the proportion of use of slope classes was equivalent to the occurrence of the classes in the polygon, pasture, or designated habitat. If H_0 was rejected, simultaneous confidence intervals for differences between percentages (Snedecor and Cochran 1967, Marcum and Loftsgaarden 1980) were derived to determine which classes were occupied at significantly ($P < 0.02$) greater than expected levels (a positive preference rating), were utilized roughly in proportion to their occurrence (a zero preference rating), or were utilized at less than expected levels (a negative preference rating).

When simultaneous comparisons are conducted within several categories, the probability that all comparisons have reached a correct conclusion is a function of the total number of comparisons made and the probability level selected for each individual comparison. The probability that all comparisons have reached a correct conclusion $= 1 - N P$ where: N is the number of categories and P is the probability level selected for the individual comparisons. If the number of categories is large and a conventional significance level of $P = 0.05$ is employed, the probability that all comparisons have reached a correct

conclusion becomes quite small. This problem may be overcome to some degree by using a more conservative significance level (i.e., $P = 0.01$). One does not wish to be so conservative, however, that real differences between percentages may go undetected, and unconventional probability levels are occasionally used as a compromise in this procedure. Because some of our data contained as many as nine categories, a probability level of $P < 0.02$ was selected for detecting differences between percentages. With nine categories there is a 0.88 probability that all of our tests have reached a correct conclusion. Neu *et al.* (1974) and Marcum and Loftsgaarden (1980) provide a more detailed discussion of the statistical processes.

Data were also pooled for each species and equations predicting the proportion of observations expected on sites with increasing slope derived through regression analysis (Neter and Wasserman 1974). F tests for comparison of two regression lines ($P < 0.05$) were conducted with all possible interspecific combinations to examine the hypothesis that patterns of slope use were identical among any of the four species (Neter and Wasserman 1974).

Results

Respective mean slopes of sites utilized by cattle, horses, deer, and bighorn were 5.8, 11.2, 15.7, and 42.5%. Data for cattle, horses, and deer were skewed in favor of relatively gentle topography, so means should be viewed with some caution. The hypothesis that each herbivore utilized classes of slopes in proportion to the topographic compositions of their respective habitats was rejected in all cases ($P < 0.01$).

Two hundred twenty-two observations of cattle were recorded, with an average group size of 14.6 animals. The greatest slope on which cattle were observed involved one sighting on a 70% grade. All other observations were on slopes of less than 40%. Patterns of slope use by cattle generally reflected those reported in the literature (Table 1). Cattle favored slopes in the 0-9% category in all pastures and appeared indifferent to slopes in the 10-19% category in pastures A and C. They avoided slopes exceeding 20% in all three pastures.

Cattle demonstrated some variation in their patterns of use among the three pastures. This is best evidenced by comparing pastures B and C which depict the extremes of topography available to these animals. Topography in pasture B was relatively gentle with a mean slope of 19%. The mean slope of pasture C was 37%, and cattle in this pasture were more often observed on the steeper slopes. This suggests that cattle inhabiting rugged terrain will make more use of steep slopes than cattle confined on more level topography. Conversely, cattle having access to large expanses of gentle topography are less likely to venture upslope than their counterparts occupying more rugged areas.

Feral horses were observed on 394 occasions, with a mean number of 4.7 animals per observation. One group of horses was observed on a 100% slope with all other observations on slopes of 50% or less. Horses generally demonstrated an affinity for high benches and gently sloping ridgetops. Typically they rapidly traversed rugged or steep topography to gain access to elevated but relatively level terrain.

The 0-19% classes in each herd received + or 0 preference ratings, indicating that slopes within this range were favored or utilized indifferently by horses (Table 1). The 20-29% category was avoided by herds 1 and 2 but used roughly in proportion to its occurrence by herd 3. Mean slopes of the habitats occupied by herds 1, 2, and 3 were 20, 24, and 34%, respectively. Like cattle, horses inhabiting rugged terrain appeared willing to utilize steeper slopes than their counterparts on more level topography. Horses in all three herds avoided slopes in excess of 30%.

One hundred seventy-two observations of deer were recorded on the area, with the average group numbering 8.5 animals. The steepest grade on which deer were detected was 75%. Like cattle and horses, deer favored relatively level topography (Table 1). They were most often observed on slopes in the 0-9% category which received a (+) preference rating. Grades between 10 and 39% appeared to have no effect on their movements, as categories in this range received (0) preference ratings. Categories in excess of 40% were utilized at significantly ($P < 0.02$) lower frequencies than their availability would suggest and received (−) preference ratings.

Bighorn sheep were observed on 121 occasions with a mean group size of 6.7 animals. Bighorn frequented grades approaching 150%,

TABLE 1. Habitat availability (%) and use (%) by cattle, horses, deer, and bighorn sheep. Categories with a (+) preference rating were utilized at greater than expected levels ($P < 0.02$). Categories having a (0) preference rating were utilized in proportion to their occurrence. Categories with a (−) preference rating were utilized at less than expected levels ($P < 0.02$).

	Percent slope								
	0-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80+
Cattle									
Pasture A availability	11	20	19	13	10	8	9	4	6
Use	79	18	3						
Preference rating	+	0	−						
Pasture B availability	23	36	24	11	2	1	3		
Use	82	15	3						
Preference rating	+	−	−						
Pasture C availability	16	17	13	14	12	10	9	3	6
Use	70	20	5	5					
Preference rating	+	0	−	−					
Horses									
Herd area 1 availability	13	31	29	14	3	3	4	1	2
Use	30	58	12						
Preference rating	+	+	−						
Herd area 2 availability	27	30	24	10	4	3	1	0	1
Use	43	41	11	4	1				
Preference rating	+	0	−	−	0				
Herd area 3 availability	13	16	19	20	12	7	5	3	5
Use	43	20	23	5	5	4			
Preference rating	+	0	0	−	−	−			
Deer									
Availability	15	18	14	14	11	9	9	3	7
Use	47	18	13	10	4	3	2	3	
Preference rating	+	0	0	0	−	−	−	−	
Bighorn sheep									
Availability	12	10	8	13	12	16	14	5	11
Use	17	8	5	8	15	11	15	14	7
Preference rating	0	0	0	0	0	0	0	+	0

but most were sited on slopes of 110% or less. The mean slope for all points sampled within the bighorn sheep habitat was 44%, while the slope of the areas actually utilized by the sheep averaged 42.5%.

The hypothesis that bighorn sheep utilized slopes in proportions equivalent to the topographic composition of their habitat was marginally rejected ($P < 0.01$). Examination of the preference ratings for each of the nine slope categories (Table 1) revealed the bighorn deviated significantly ($P < 0.02$) from our expected pattern of use in only one instance (the 70-79% category). Because this category received a (+) preference rating, and all other categories were frequented at expected levels, we concluded that slopes between 0 and 80% did not impair the movements and activities of bighorn.

Second-order equations provided best fit of data relating percent slope (independent variable) to percent of observations of herbivores in each category (dependent variable). Significant response functions ($P < 0.05$) were obtained for cattle ($Y = -6.0X + 0.09X^2 + 96.4$, $r^2 = 0.95$), horses ($Y = -1.9X + 0.02X^2 + 54.4$, $r^2 = 0.96$), and deer ($Y = -1.5X + 0.01X^2 + 45.9$, $r^2 = 0.89$) but no significant relationship was derived for bighorn sheep (Figure 1). Our attempt to fit a second-order polynomial to the bighorn sheep data produced an r^2 of 0.22 and an F value of 0.98. This again suggests that slopes between 0 and 80% had no effect on the habits of bighorn sheep.

Our F tests for all possible interspecific comparisons of two regression lines rejected the hypothesis that patterns of slope use were identical among cattle, horses, and deer ($P < 0.01$). Although each equation proved to be unique, we do not intend to infer that a clear spatial separation existed between the various species.

Discussion

Slopes between 0 and 19% received either (+) or (0) preference ratings in our analysis of all four herbivores. These same slopes supported 94% of our observations of cattle, 79% of the horses, 66% of the deer, and 25% of the bighorn sheep. It is obvious that cattle, horses, and deer exerted the majority of their demands on the resources occurring within these bounds. Bighorn sheep, with their greater tolerance or preference for steep slopes, were much less dependent on the resources of relatively gentle terrain.

These data clearly illustrate that in rugged terrain cattle, horses, and deer will limit their use of steep sidehills. Consequently, range managers and researchers need to consider the effects of varying topography on the distribution patterns of these animals.

Due to several factors, however, caution must be exercised when applying these results to other areas. Our first concern is that much of our data were of a seasonal nature. We recognize that

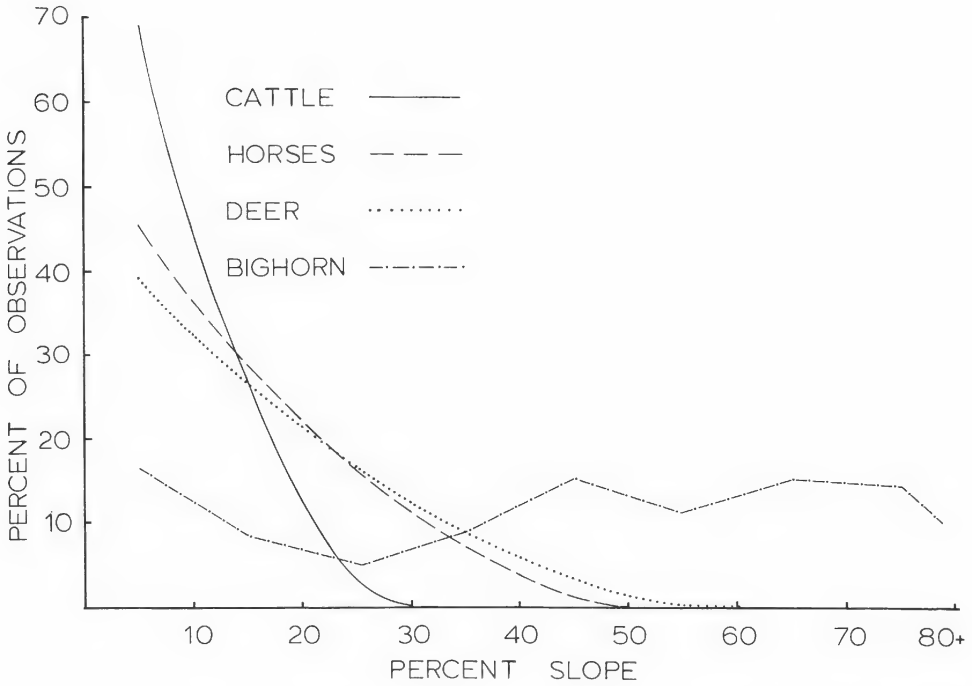

Figure 1. Relationship of slope gradient to the percent of observations of cattle, feral horses, deer, and bighorn sheep. Raw data are presented for bighorn sheep because a significant ($P < 0.05$) relationship could not be obtained with linear or quadratic models.

patterns of use are subject to change throughout the year. In this study, cattle in particular appeared more willing to utilize slopes in the early spring and late fall, than during the warmer summer months. Our sample numbers, however, were too small to address this hypothesis with any statistical confidence.

A second consideration is that our observations relate to populations having access to a common environment. We saw no aggressive behavior during interspecific encounters, but competitive processes or interspecific intolerances may have altered dispersion patterns to some degree (Berger 1985). If such competitive influences were present, our data may reflect an up-slope movement of one or more of the herbivores in question.

Our third concern focuses on the different patterns of use exhibited by cattle and horses when comparing relatively gentle and more rugged habitats. This suggests that quantitative expectations derived in one area may not necessarily apply in another. We recognize that each management unit provides a unique environment, and that patterns of animal movement are ultimately a product of several interacting environmental and animal factors. Although much more data must be acquired before these variations in utilization patterns can be described with any confidence, we should remain aware that topographic attributes may limit resource use by cattle, deer, and feral horses.

Literature Cited

Barrett, R. H. 1982. Habitat preferences of feral hogs, deer, and cattle on a Sierra foothill range. J. Range Manage. 35:342-346.

Berger, J. 1985. Interspecific interactions and dominance among wild great basin ungulates. J. Mammal. 66:571-573.

Blood, D. A. 1961. An ecological study of California bighorn sheep in southern British Columbia. University of British Columbia, Vancouver. Thesis.

Bryant, L. D. 1982. Response of livestock to riparian zone exclusion. J. Range Manage. 35:780-785.

Champline, W. R., and M. W. Talbot. 1926. The use of salt in range management, U.S. Dept. Agr. Dept. Circ. 379.

Cook, C. W. 1966. Factors affecting utilization of mountain slopes by cattle. J. Range Manage. 19:200-204.

Demarchi, R. A. 1965. An ecological study of the Ashnola bighorn winter ranges. University of British Columbia, Vancouver. Thesis.

Dusek, G. L. 1975. Range relations of mule deer and cattle in prairie habitat. J. Wildl. Manage. 39:605-616.

Ganskopp, D. C. 1984. Habitat use and spatial interactions of cattle, wild horses, mule deer, and California bighorn sheep in the Owyhee Breaks of southeast Oregon. Oregon State University, Corvallis. Dissertation.

Ganskopp, D. C., and M. Vavra. 1986. Habitat use by feral horses in the northern sagebrush steppe. J. Range Manage. 39:207-211.

Gilbert, P. E., O. C. Wallmo, and R. B. Gill. 1970. Effect of snow depth on mule deer in Middle Park, Colorado. J. Wildl. Manage. 34:15-23.

Gillen, R. L. 1982. Grazing behavior and distribution of cattle on mountain rangelands. Oregon State University, Corvallis. Dissertation.

Glendening, G. E. 1944. Some factors affecting cattle use of northern Arizona pine-bunchgrass ranges. U.S. Dept. Agr.; For Serv., SW For. and Range Exp. Sta. Res. Rep. 6.

Gonzalez, M. H. 1964. Patterns of livestock behavior and forage utilization as influenced by environmental factors on a summer mountain range. Utah State University, Logan. Dissertation.

Harris. J. T. 1956. Survey of the Poudre River bighorn herd. Colorado Coop. Wildl. Res. Unit, Quarterly Report. 10:25-33.

Jones, F. L. 1980. Competition. *In* G. Monson, and L. Sumner (eds.) The desert bighorn: its life history, ecology, and management. University Arizona Press, Tucson. Pp. 197-216.

Julander, O. 1966. How mule deer use mountain rangeland in Utah. Utah Academy of Sciences, Arts, and Letters. 43:22-28.

Julander, O., and D. E. Jeffery. 1964. Deer, elk, and cattle range relations on summer range in Utah. Trans. N. Am. Wildl. and Nat. Res. Conf. 29:404-414.

Keiper, R. R., and J. Berger. 1982. Refuge-seeking and pest avoidance by feral horses in desert and island environments. Applied Animal Ethology 9:111-120.

Loveless, C. M. 1967. Ecological characteristics of a mule deer winter range. Colorado Game, Fish and Parks Dept. Tech. Bull. 20.

Mackie, R. J. 1970. Range ecology and relations of mule deer, elk, and cattle in the Missouri River Breaks, Montana. Wildl. Monogr. 20.

Marcum, C. L., and D. O. Loftsgaarden. 1980. A non mapping technique for studying habitat preference. J. Wildl. Manage. 44:963-968.

McCann, L. J. 1953. Ecology of the mountain sheep. University of Utah, Salt Lake City. Dissertation.

McCullough, D. R., and E. R. Schneegas. 1966. Winter observations on the Sierra Nevada bighorn sheep. California Fish and Game. 52:68-84.

Miller, R. 1980. The ecology of feral horses in Wyoming's Red Desert. University of Wyoming, Laramie. Dissertation.

Mueggler, W. F. 1965. Cattle distribution on steep slopes. J. Range Manage. 18:255-257.

Neter, J., and W. Wasserman. 1974. Applied linear statistical models. R. D. Irwin, Inc. Homewood, Illinois.

Neu, C. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. J. Wildl. Manage. 38:541-545.

Patton, W. W. 1971. An analysis of cattle grazing on steep slopes. Brigham Young University, Provo, Utah. Thesis.

Pelligrini, S. W. 1971. Home range, territoriality and movement patterns of wild horses in the Wassuk Range of western Nevada. University of Nevada, Reno. Thesis.

Phillips, T. A. 1965. The influences of slope gradient, distance from water, and other factors on livestock distribution on national forest cattle allotments of the Intermountain region. U.S. Dept. Agr.-For. Serv. Intermount. For. and Range Exp. Sta., Range Improvement Notes 10(3):9-19.

Russo, J. P. 1956. The desert bighorn sheep in Arizona. Arizona Game and Fish Dept. Wildl. Bull. No. 1 W-53-R.

Shannon, N. H., R. J. Hudson, V. C. Brink, and W. D. Kitts. 1975. Determinants of spatial distribution of Rocky mountain bighorn sheep. J. Wildl. Manage. 39:387-401.

Skovlin, J. M. 1965. Improving cattle distribution on western mountain grasslands. U.S. Dept. Agr. Farm Bull. No. 2212.

Snedecor, G. W., and W. C. Cochran. 1967. Statistical methods. Iowa State University Press. Ames, Iowa.

Southwood, T. R. E. 1966. Ecological methods with particular reference to the study of insect populations. Methuen & Co., London.

Todd, J. W. 1972. Food habits of Rocky Mountain bighorn sheep. Colorado State University, Fort Collins. Thesis.

Van Vuren, D. 1982. Comparative ecology of bison and cattle in the Henry Mountains, Utah. *In* J. M. Peek, and P. D. Dalke (eds.) Proc. Wildlife-Livestock Relationships Symp., Dept. of Wildlife Resources, College of Forestry, Wildlife and Range Sciences, University of Idaho, Moscow. Pp. 449-457.

Welsh, D. A. 1975. Population, behavioral, and grazing ecology of the horses of Sable Island, Nova Scotia. Dalhousie, University. Dissertation.

Wilkins, B. T. 1957. Range use, food habits, and agricultural relationships of the mule deer, Bridger Mountains, Montana. J. Wildl. Manage. 22:159-169.

Received 4 June 1986
Accepted for publication 23 October 1986

David A. Manuwal, Mark H. Huff, Michael R. Bauer, Christopher B. Chappell, and **Karen Hegstad**
Wildlife Science Group, College of Forest Resources, University of Washington, Seattle, WA 98195

Summer Birds of the Upper Subalpine Zone of Mount Adams, Mount Rainier, and Mount St. Helens, Washington

Abstract

Fifty-five bird species were observed during the summers of 1982 and 1985 using the upper subalpine habitat on three Cascade volcanoes. The vegetation differed somewhat among the study areas, although subalpine fir (*Abies lasiocarpa*) was the dominant tree at all sites. Bird species richness was highest at Mount Adams and Pine Creek on Mount St. Helens, and lowest at Butte Camp on Mount St. Helens. Bird abundance was highest at Butte Camp where there were large numbers of pine siskins. Several species exhibited wide variation in abundance among study areas. Approximately 18 species nested at each study area, but there was variation in species composition. Differences in abundance and species composition were partly attributable to vegetation features of the study areas. Birds feeding on insects on or near the ground, and conifer seed-eaters were numerically dominant. There appeared to be no longterm impact of the 1980 eruption of Mount St. Helens on the subalpine avifaunas except at Pine Creek where the trees were scorched and subsequently died.

Introduction

The large dominant volcanic peaks, Mount Rainier, Mount Adams, and Mount St. Helens, in the Washington Cascade Range are part of a belt of active volcanoes surrounding the Pacific Ocean (Bullard 1979). The particular species composition and structure of subalpine forest communities on these volcanoes and the bird assemblages that depend on them have been shaped by previous volcanism and geographic location. Although these peaks, particularly Mount Rainier, have been previously studied by botanists, we are unaware of any previously-published studies on bird communities in the upper subalpine zone of the Cascades.

Subalpine bird communities have been investigated in other parts of the United States (e.g., Rabenold 1978, Sabo 1980, Smith 1980, Kendeigh and Fawver 1981, Smith and MacMahon 1981). In general, these studies have shown that high-elevation forest avifaunas show marked differences in some characteristics compared with lower elevation forests.

This study was initiated as part of an interdisciplinary investigation on the effects of the 1980 eruptions of Mount St. Helens on plants, animals, and soils. Since nearly all the subalpine zone of Mount St. Helens was destroyed or disturbed by the 1980 eruptions, we selected undisturbed subalpine sites on Mount Adams to the east and Mount Rainier to the north for comparison. This allowed us a broader perspective of subalpine bird communities in the Cascades.

The specific questions asked were: (1) how do avian species composition and abundance on Mount St. Helens compare with those on Mount Adams and Mount Rainier? and (2) what were the effects of the 1980 eruptions on the summer birds of the upper subalpine zone of Mount St. Helens?

Study Area

We use the term subalpine to refer to the tree-dominated montane forests that border the upper elevation treeless zones (MacMahon and Andersen 1982). On the western slopes and crest of the Cascade Range, this forest is classified as the Mountain Hemlock Zone (Franklin and Dyrness 1973). This zone has been divided into two major subzones: a lower one that is a nearly closed canopy forest, and an upper one that is a meadow-forest mosaic. Two of our study sites (Sunrise and Butte Camp) were in the upper subzone, one was in the lower subzone (Killen Creek), and one (Pine Creek) incorporated features of both subzones. Even though all study sites were in the subalpine zone, tree species composition, relative abundance (Table 1), and understory vegetation (Table 2) varied among the four areas. We first tested these differences by using one-way ANOVA, followed by Students t tests for comparisons between individual areas (Colton, 1974).

The Butte Camp site (elevation, 1360 m), at treeline on the southwest flank of Mount St. Helens, was dominated by a mixture of small-sized subalpine fir (*Abies lasiocarpa*) and

TABLE 1. Characteristics of the subalpine forest censused on Mount St. Helens, Mount Adams, and Mount Rainier, Washington.

	Mount St. Helens								Mount Adams				Mount Rainier			
	Pine Creek				Butte Camp				Killen Cr.				Sunrise			
			DBH(cm)				DBH(cm)				DBH(cm)				DBH(cm)	
	N	D*	$\bar{X}$	SD	N	D	$\bar{X}$	SD	N	D	$\bar{X}$	SD	N	D	$\bar{X}$	SD
Subalpine Fir *Abies lasiocarpa*	110	58	21.0	15.1	76	124	8.4	8.3	80	63	21.7	15.2	147	16	22.2	16.8
Lodgepole Pine *Pinus contorta*	27	14	13.1	12.7	72	117	6.5	6.1	36	28	11.3	10.3				
W. White Pine *P. monticola*	2	1	31.9	3.6	4	6	9.3	12.3	15	12	7.3	4.7				
Whitebark Pine *P. albicaulis*													9	1	24.2	13.8
Mountain Hemlock *Tsuga mertensiana*									27	21	19.4	11.5	1			
Pacific Silver Fir *Abies amabilis*	19	10	6.9	2.8												
Noble Fir *A. procera*					8	13	3.2	0								
Englemann Spruce *Picea engelmannii*									2	2	26.0	7.1				
TOTAL	158	83			160	260			160	125			157	17		

*D is density (trees/ha)

TABLE 2. Mean percent cover and height (cm) of understory vegetation at subalpine study sites in the Southern Washington Cascade Mountains. Values in bold and bold italic are not significantly different ($P > .05$)

	Mount St. Helens				Mount Adams		Mount Rainier	
	Butte Camp		Pine Creek		Killen Creek		Sunrise	
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Percent herb cover	2.5	2.9	**12.8**	**13.1**	**10.4**	**8.7**	34.1	17.4
Percent woody cover	***6.5***	***12.8***	**30.3**	**24.2**	**30.3**	**17.5**	***4.8***	***13.3***
Height of herbs	3.9	2.7	10.1	8.6	**16.2**	**5.2**	**16.2**	**7.9**
Height of woody plants	**26.5**	**30.8**	**36.5**	**21.3**	47.2	13.7	8.4	19.8

[a]$P < 0.001$

lodgepole pine (*Pinus contorta*). A few western white pines (*P. monticola*) and noble firs (*A. procera*) were also present. During the 1980 eruptions this area received a layer of airborne tephra as well as two mudflows near the site. The trees showed no obvious effect from the eruptions. The sparse ground vegetation, however, was impacted even though it was under snow when the large eruption occurred in May. There was some reduction in plant species diversity and ground cover, but by 1982 it had recovered substantially (del Moral 1983).

The Pine Creek site (elevation 1,650 m) was also at treeline on the southeast flank of Mount St. Helens at the edge of the large Pine Creek mudflow. The tree species composition and structure of this area was an ecotone between the upper and lower subzones of mountain hemlock

(*Tsuga heterophylla*). As at Butte Camp, the upper subzone is very narrow in vertical extent there. The study area was a mixture of several conifer species dominated primarily by live and lethally-scorched subalpine firs. Pacific silver fir (*A. amabilis*) was abundant in the understory of the lower subzone and less numerous in the overstory. Lodgepole pine, which thrived on the xeric volcanic soils, was important in the upper subzone. Western white pine and noble fir were frequent in the lower subzone overstory. Tree heights varied more than those at any site: at treeline subalpine firs and lodgepole pines were 2 m tall whereas 300 m downslope trees were 20 m tall. Ground vegetation was lush in the lower subzone, being dominated by lupine (*Lupinus latifolius*) and huckleberry (*Vaccinium membranaceum*).

The Killen Creek site (elevation 1,650 m) was on the north side of Mount Adams in the lower subzone. The dominant trees were subalpine fir and lodgepole pine. The forest is broken by many small openings that are densely choked with *V. membranaceum,* indicating that the stand may be a slowly-developing fire-related seral stage (Franklin and Dyrness 1973). The dominant shrub was *V. membranaceum.* This stand has elements of the Mountain Hemlock Zone of the upper west slope of the Cascades and the Subalpine Fir Zone typical of the eastern upper slope of the Cascades. Tree density was intermediate between the two Mount St. Helens sites.

The Sunrise site (elevation 2,100 m) was on the northeast slope of Mount Rainier in the upper subzone. This subalpine environment differed from the other sites in that it was at a higher elevation, the trees were arranged in widely-spaced clumps, and whitebark pine (*P. albicaulis*) replaced lodgepole pine. The open meadows between tree clumps were dominated by a variety of primarily herbaceous plants.

Methods

Trees were sampled by using the point-centered quarter method (Mueller-Dombois and Ellenberg 1974). Forty points were spaced along the bird point-count route in each study area. Understory cover was estimated using a 1 m square frame made of PVC tubing. Four quadrats were placed 1 m from the station point marker in the four cardinal directions, making a total of 48 quadrats in each study area.

Originally, we used the variable circular plot technique (Reynolds *et al.* 1980) to estimate bird densities. However, we found this method unsuitable because of logistical constraints, the presence of uncommon species, and relatively large numbers of flocking birds for which no density estimate could be calculated. We therefore estimated relative abundance by a station count method in which we established 11-22 stations spaced 100 m apart, usually along a rectangular route. All birds seen or heard during an eight-minute period at each station were recorded and a mean detection rate was calculated by dividing total number of observations by total number of station counts for six visits. Observer discretion was used to avoid double counting. Preliminary observations were made by Manuwal in 1981. All data reported are for 30 June-30 August 1982 and 8 July-26 August 1985.

Coefficients of species similarity (Ss) were calculated with the Sorenson equation (Able and Noon 1976):

$$Ss = 2C/(A + B)$$

where C represented the species common to the two subalpine habitats, and A and B the number of bird species in each habitat. Values higher than 0.50 indicate that the two habitats are more alike than different.

We also evaluated the abundance pattern by using a coefficient of population similarity (Sp) (Odum 1950):

$$Sp = 1.0 - \Sigma(Pa - Pb) / Pa + Pb$$

where Pa is the population of a species in habitat a and Pb in habitat b, + ΣPa and Pb are the total populations (sum of detection rates in Table 3) in the two habitats. Differences in detection rates among the four study areas were tested by using one-way analysis of variance. The birds using our study areas were classified into nine general foraging guilds similar to those described by Smith (1982) and Sabo and Holmes (1983).

Results

Vegetation Parameters—Subalpine fir was the dominant tree species on all study areas (Table 1) and the only species to occur at all study sites. Lodgepole pine was a codominant at Butte Camp and was the second most abundant species at Pine Creek (except in the lower subzone) and Killen Creek. Western white pine also occurred

TABLE 3. Sampling effort, species richness, and abundance of summer birds of subalpine forests of Mount St. Helens, Mount Adams, and Mount Rainier, Washington

Category	Mount St. Helens		Mount Adams	Mount Rainier
	Pine Creek	Butte Camp	Killen Creek	Sunrise
Number of station Counts[a]	184	160	248	224
Total Observations	1278	1354	1845	1427
Total Species	43	35	44	30
Detection Rate[b]	6.92	8.53	7.41	6.44
Mean Detection Rate/Species	0.16	0.24	0.17	0.21
Breeding Species	23	12	18	18
Detection Rate	6.57	7.55	6.64	5.71
Mean Detection Rate/Species	0.27	0.63	0.37	0.32

a Product of the number of stations and the number of visits.
b Mean number of birds detected per station count.

at three of the four sites. Several other conifers were unique to each particular site. Tree density ranged from 260 trees/ha at Butte Camp to 17 trees/ha at Sunrise (Table 1). Mean diameter of trees was smaller ($t = 2.58$, $P < .001$) at Butte Camp than at the other three sites.

Understory vegetation varied among study areas (Table 2). Of the study area cover comparisons, all but Pine Creek-Killen Creek differed ($t = 1.08$, $P = 0.28$) in the amount of herbaceous vegetative cover. Furthermore, only Pine Creek-Killen Creek ($t = 0.005$, $P = 0.99$) and Butte Camp-Sunrise ($t = 0.64$, $P = 0.52$) did not differ in woody vegetation cover. All but Sunrise-Killen Creek differed ($t = 1.53$, $P = 0.99$) in herbaceous vegetation height and Butte Camp-Pine Creek differed ($t = 1.86$, $P = 0.07$) in woody vegetation height.

Avian Communities—Due to the extreme variation in breeding phenologies of birds in the Cascade Range, two analyses of the data were necessary to better understand summer birds using subalpine habitats. At the time of our study, two major groups of birds were using the upper subalpine. These were (1) birds nesting on our study areas and (2) visitors that had already completed nesting at lower elevations and were dispersing or migrating upslope. It was, of course, difficult to identify the breeding status of individual birds observed. Nevertheless, based on observations of nests, adults feeding young, and literature references, we were able to determine which species were breeding or were most likely to breed on our study areas. Our analyses, therefore, will first consider all bird observations and then the breeding species.

All birds observed—During 1982 and 1985 we observed 55 species on the study areas. Species richness was highest at Killen Creek and Pine Creek and lowest at Sunrise (Table 3). The relatively low diversity of these communities was reflected by avian dominance values (the two most abundant species as a percent of the total). These were 59% for Butte Camp, 45% for Sunrise, 39% for Killen Creek, and 37% for Pine Creek.

There were substantial differences in species composition among the four study areas (Table 4). Coefficients of similarity (Ss) were low ($\bar{X} = 0.35$) for the six comparisons. These low coefficients reflect the relatively large number of uncommon species detected at each of the sites. For example, the percentages of all species with detection rates of 0.05 or less were 61% for Killen Creek, 56% for Pine Creek, 54% for Butte Camp, and 30% for Sunrise (Appendix).

Total detection rates differed ($P < 0.001$) among the four study areas. Furthermore, there were large differences in abundance of individual species. For example, Clark's nutcrackers and evening grosbeaks were far more common at Killen Creek and Sunrise than the sites on Mount St. Helens (Appendix). Flocking species such as pine siskin, evening grosbeak, and crossbills showed wide variation in abundance among the four study areas.

Pine siskins and dark-eyed juncos were the most abundant birds, comprising 44% of all bird

TABLE 4. Species richness and similarity coefficients (Sp, Ss) among subalpine bird populations in the southern Washington Cascade Mountains

Locations	Species Common to both areas		Similarity			
			All species		Breeding	
	All species	Breeding species	Sp	Ss	Sp	Ss
Pine Creek-Killen Creek	32	11	0.71	0.26	0.61	0.39
Killen Creek-Sunrise	26	14	0.69	0.39	0.70	0.36
Butte Camp-Sunrise	23	11	0.63	0.37	0.63	0.32
Butte Camp-Killen Creek	27	11	0.62	0.37	0.63	0.34
Pine Creek-Butte Camp	30	12	0.56	0.33	0.55	0.37
Pine Creek-Sunrise	23	12	0.55	0.31	0.45	0.34
$\bar{X}$	26.8	11.8	0.63	0.34	0.60	0.35

observations (N = 5904). They were the dominant species in all areas except at Pine Creek in 1982 when white-crowned sparrows were more numerous.

Breeding birds—Thirty-two bird species nested on study areas. On average, there were 18 nesting species at each study area (Table 3). The four study areas differed substantially in breeding species composition, having low coefficients of species similarity (Ss) ($\bar{X}$ = 0.34) (Table 4). However, when abundance was included in the comparisons, coefficients of population similarity (Sp) were relatively high for all comparisons, indicating that nesting populations were similar in size. The mean breeding species component was about 44% of all birds detected.

In terms of abundance, low understory and ground insectivores (LUGI) and tree-seed eaters (TS) were the largest guilds using these subalpine areas (Fig. 1). These foraging guilds were dominant at all sites except Pine Creek where the TS guild was depauperate. At Pine Creek few trees were available for foraging due to the destructive force of the 1980 eruption. Pine Creek had the highest percentage (62) of birds in the LUGI guild, dominated by dark-eyed juncos and white-crowned sparrows. This guild was about 50% smaller at the other three sites.

Discussion

The particular assemblages of species at each site were probably the result of habitat structure, tree-seed production, and climate. The harsh weather conditions typical of the upper subalpine zone shape the structural features of subalpine forests (Arno and Hammerly 1984). Structural attributes of subalpine and other forests have been linked with avian niche development (Holmes *et al.* 1979, Sabo 1980, Maurer and Whitmore 1981). The large differences in vegetative features could account for the relatively low coefficients of similarity among the four areas. Conversely, Pine Creek and Killen Creek were most similar in vegetative attributes and breeding avifauna.

Despite the dominance of subalpine fir at all study sites, the presence of other tree species undoubtedly affected bird abundance as well as guild development. The presence of pines, particularly whitebark pine and other seed-bearing conifers support the TS guild. For example, the Clark's nutcracker is a specialized seedeater that utilizes large seeds of pines (Mewaldt 1956, Tomback 1977). Nutcrackers nested only at Mount Rainier and Mount Adams where whitebark pine occurred on the study area. The large number of crossbills and possibly pine siskins were most likely linked with the abundance of seed-bearing trees. In our study and others (Smith 1980) pine siskins were a common element of western subalpine forests. Wiens (1975) and Smith (1980) found that seed-eating species were the dominant avian groups foraging in subalpine trees.

The adverse climate and the reduced resources associated with the relatively small trees typical of upper subalpine areas in the Cascades apparently affect the number of birds that search for insects in tree foliage. There is a paucity of warblers, flycatchers, and woodpeckers in these subalpine forests. The typical warbler of the subalpine was the yellow-rumped,

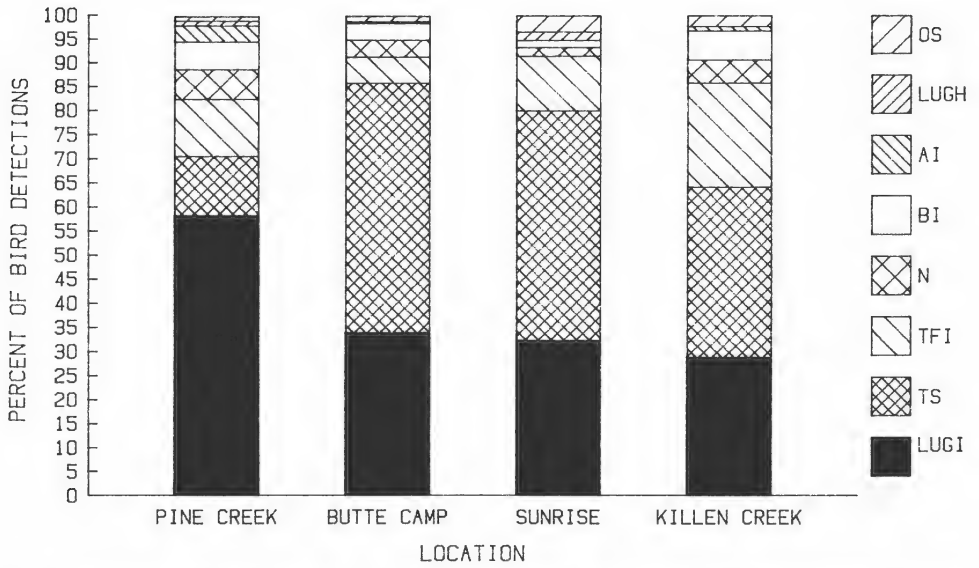

Figure 1. Histograms showing proportion of birds in each of nine feeding guilds at four subalpine sites in the Washington Cascades. Guilds are as follows: OS = omnivore-scavenger, LUGH = low understory and ground herbivore, AI = aerial insectivore, BI = bark insectivore, N = nectivore, TFI = tree foliage insectivore, TS = tree-seed eater, LUGI = low understory and ground insectivore.

which was observed consistently in all study areas. Townsend's and the yellow-rumped are the common warblers dwelling in the tree canopy of the higher elevations on the east slope of the Cascades.

Although flycatchers were present, they were rare, olive-sided being the most common. Apparently the lack of flycatchers reflects either an inadequate supply of flying insects or some unfavorable structural features of the forests. Flycatchers were also uncommon in northeastern subalpine forests (Sabo 1980, Sabo and Holmes 1983) and in the Rocky Mountain subalpine forests (Smith 1980, Smith and MacMahon 1981).

Low numbers of woodpeckers are probably due to small tree and snag size and high wood density of the slow-growing subalpine conifers. Although we did not sample bark insects, the small woodpecker populations may have been limited by lack of wood-boring insects. Red-breasted nuthatches, which nested in the study areas, forage on the trunk and on branches and needle clusters where they presumably exploit a *different group* of insects than woodpeckers. This may explain why this species was the most common member of the bark insectivore (BI) guild in our study areas.

Data on understory cover and height did not explain differences in abundance and guild development. The LUGI guild was well-developed in all areas despite wide variation in cover and height values. Furthermore, understory characteristics of Pine Creek and Killen Creek were similar, yet there were substantial differences in abundance and species composition within the LUGI guild. Why white-crowned sparrows were common breeders at Pine Creek and not at Killen Creek; and why fox sparrows were nesting at Killen Creek but not at Pine Creek remains unexplained. Other habitat features such as plant species composition or dispersion of conifers may have affected birds using the ground or understory vegetation.

An interesting distributional pattern was evident with the purple finch, typical of the lower elevation coniferous forests on the west slope of the Cascades, and the Cassin's finch, more typical of the east slope of the Cascades. We observed

Cassin's finches breeding in all study areas, including Mount St. Helens which is west of the Cascade Crest. Purple finches did not occur in numbers until August, after the lowland breeding season. This pattern suggests that the Cassin's finch is the more typical upper subalpine red finch of either slope.

Only one species appeared to be strongly characteristic of one subzone or the other. The chipping sparrow was much more numerous in the upper subzone than the lower and nested only in the upper subzone. The species may be responding to the mosaic of meadows and tree clumps. This structural feature is also present in other Washington state habitats such as the ponderosa pine forests of eastern Washington, where chipping sparrows are common.

Finally, the effect of the 18 May 1980 eruption of Mount St. Helens on the bird populations varied according to the amount of devastation. Butte Camp, which received only a light tephra fall, and where the birds probably dispersed for a short time (Butcher 1981), had a bird community with foraging guilds similar to Killen Creek on Mount Adams, even though the physical appearances of the stands differ.

Pine Creek, although out of the area of high devastation, was nonetheless dramatically impacted by the hot gas eruption of July 1980 that scorched the forest. Some birds were probably killed outright, but the greatest impact occurred because the vegetation was destroyed. This resulted in the loss of the tree foliage insectivore (TFI) and TS foraging guild substrates and the dramatic reductions of birds using these guilds in comparison with the other sites. The few birds in these guilds were in the lower vertical strata that escaped the scorching. The avifauna occupying the scorched forest area two and five years after the eruption was dominated by birds using the ground and understory vegetation, for example, dark-eyed juncos, white-crowned sparrows, and rufous hummingbirds.

Approximately half the upper subalpine forests of Mount St. Helens were destroyed in the 18 May 1980 eruption. This eruption instantly killed the majority of birds present in these areas. Those birds included permanent residents, winter residents, and early migrants. This area will probably be re-colonized as the vegetation becomes re-established. Presumably, birds using ground vegetation and aerial insects will colonize first (e.g., white-crowned sparrow, dark-eyed junco, mountain bluebird, common nighthawk, (*Chordeiles minor*). This process is already beginning but re-colonization of birds in all foraging guilds, in proportion to the other sites, will probably take many years.

The subalpine forests of the Washington Cascade volcanoes vary in tree species composition, structure, and elevational limits. Bird species composition and abundance patterns show predictable patterns relative to geographical location, general forest structure, and amount of volcanic disturbance. More research is justified to further delineate patterns of distribution and resource use and partitioning in the upper subalpine forest.

Acknowledgments

We thank the U.S. Forest Service, Randle District, Gifford Pinchot National Forest, and the National Park Service, Mount Rainier National Park, particularly S. Schlegel, for permission to visit the areas under their jurisdiction. We thank the National Science Foundation for the grant to L. C. Bliss, Department of Botany, University of Washington for financial support. We are indebted to N. J. Manuwal, C. Braun and K. Smith and two anonymous reviewers for their editorial comments on the manuscript.

Appendix. Detection rates (mean number detected per station count) of summer birds of subalpine forests of Mount St. Helens, Mount Adams and Mount Rainier, Washington.

Guild and species	Mount St. Helens		Mount Adams	Mount Rainier
	Pine Creek	Butte Camp	Killen Creek	Sunrise
Aerial Insectivores (AI)				
Olive-sided Flycatcher *Contopus borealis*	0.14**	0.01	0.04	

Appendix continued

Guild and species	Mount St. Helens		Mount Adams	Mount Rainier
	Pine Creek	Butte Camp	Killen Creek	Sunrise
Western Wood-Pewee *C. sordidulus*	0.01			
Willow Flycatcher *Empidonax trailii*	0.01			
Western Flycatcher *E. difficilus*	0.08**	0.01	0.02	
Empidonax sp.		0.02		
Rough-winged Swallow *Stelgidropteryx serripennis*	0.01			
Tree Foliage Insectivores (TFI)				
Mountain Chickadee *Parus gambeli*		0.01	0.48**	0.29**
Chestnut-backed Chickadee *P. rufescens*	0.03**		0.01	
Golden-crowned Kinglet *Regulus satrapa*	0.33**	0.21**	0.20**	0.07
Ruby-crowned Kinglet *R. calendula*			0.02**	
Solitary Vireo *Vireo solitarius*			0.01	
Warbling Vireo *V. gilvus*	0.01**		+***	
Orange-crowned Warbler *Vermivora celata*	0.06		0.04	0.01
Nashville Warbler *V. ruficapilla*	0.01		0.21	
Yellow-rumped Warbler *Dendroica coronata*	0.25**	0.20**	0.58**	0.32**
Townsend's Warbler *D. townsendi*	0.01		0.05	0.01
Hermit Warbler *D. occidentalis*	0.03**	0.01	0.02	
Hermit or Townsend's Warbler	0.03	0.01	0.02	0.01
Western Tanager *Piranga ludoviciana*	0.06**	0.03	+	0.01
Black-headed Grosbeak *Pheucticus melanocephalus*		0.01		
Tree-seed Eaters (TS)				
Clark's Nutcracker *Nucifraga columbiana*		0.01	0.53**	0.39**
Red Crossbill *Loxia curvirostra*	0.03	0.39	0.16**	0.11
White-winged Crossbill *L. leucoptera*	0.02	0.11	0.18	0.15
Pine Siskin *Carduelis pinus*	0.66**	3.41**	1.30**	1.83**

Appendix continued

Guild and species	Mount St. Helens		Mount Adams	Mount Rainier
	Pine Creek	Butte Camp	Killen Creek	Sunrise
Pine Grosbeak *Pinicola enucleator*			+	
Purple Finch *Carpodacus purpureus*	0.03	0.05	0.01	+
Cassin's Finch *C. cassinii*	0.02**	0.31**	0.18**	0.09**
Purple or Cassin's Finch	0.02	0.02	0.03	
Evening Grosbeak *Coccothraustes vespertinus*	0.08	0.09	0.19**	0.51**
Bark Insectivores (BI)				
Hairy Woodpecker *Picoides villosus*	0.02		0.02**	
Williamson's Sapsucker *Sphyrapicus thyroideus*	.01			
Red-breasted Nuthatch *Sitta canadensis*	0.39**	0.29**	0.43**	0.09**
Low Understory and Ground Insectivores (LUGI)				
Northern Flicker *Colaptes auratus*	0.23**	0.07	0.08	0.06**
House Wren *Troglodytes aedon*			0.01	
Winter Wren *T. troglodytes*	0.30**	0.01	+	0.05
Mountain Bluebird *Sialia currucoides*	0.08**	0.04		
Hermit Thrush *Catharus guttatus*	0.18**	0.08**	0.10**	0.05**
American Robin *Turdus migratorius*	0.37**	0.57**	0.33**	0.21**
Varied Thrush *Ixoreus naevius*	0.26**	0.31**	0.03**	0.04**
Townsend's Solitaire *Myadestes townsendi*		0.01		
Wilson's Warbler *Wilsonia pusilla*	0.01	0.03	0.02	
MacGillivray's Warbler *Oporornis tolmei*	0.04		+	
Chipping Sparrow *Spizella passerina*	0.04**	0.38**	0.04	0.37**
Fox Sparrow *Passerella iliaca*			0.05**	0.10**
White-crowned Sparrow *Zonotrichia leucophrys*	0.72**	0.01		

Appendix continued

Guild and species	Mount St. Helens		Mount Adams	Mount Rainier
	Pine Creek	Butte Camp	Killen Creek	Sunrise
Dark-eyed Junco *Junco hyemalis*	1.83**	1.40**	1.59**	1.06**
Low Understory and Ground Herbivores (LUGH)				
Blue Grouse *Dendragapus obscurus*	0.07**	0.01		0.12**
Nectivores (N)				
Black-chinned Hummingbird *Archilochus alexandri*	0.01			
Calliope Hummingbird *Stellula calliope*				+**
Rufous Hummingbird *Selasphorus rufus*	0.43**	0.31**	0.35**	0.11**
Omnivore-Scavengers (OS)				
Gray Jay *Perisoreus canadensis*	0.05**	0.08**	0.10**	0.07**
Steller's Jay *Cyanocitta stelleri*			0.05	
Common Raven *Corvus corax*	0.02	0.01	0.01	0.17
Carnivores (C)				
Sharp-shinned Hawk *Accipiter striatus*				+
Unidentified accipiter	0.01			0.01
Northern Goshawk *A. gentilis*		0.01		
Red-tailed Hawk *Buteo jamaicensis*			+	
Golden Eagle *Aquila chrysaetos*			+	
American Kestrel *Falco sparverius*	0.01			0.01
Northern Pygmy Owl *Glaucidium gnoma*	0.01			

**Nested in the study area.
***Detection rate was less than <0.01.

Literature Cited

Able, K. P., and B. R. Noon. 1976. Avian community structure along elevational gradients in the northeastern United States. Oecologia 26:275-295.

Arno, S. F., and R. P. Hammerly. 1984. Timberline. Mountain and Arctic Forest Frontiers. The Mountaineers, Seattle, Washington.

Bullard, F. 1979. Volcanoes and their activity. *In* P. Sheets and D. Grayson (eds.) Volcanic Activity and Human Ecology. Academic Press, New York, New York.

Butcher, G. 1981. Northern Orioles disappear with Mount St. Helens ashfall. Murrelet 62:15-16.

Colton, T. 1974. Statistics in medicine. Little, Brown and Co., Boston.

del Moral, R. 1983. Initial recovery of subalpine vegetation on Mount St. Helens, Washington. Amer. Midl. Nat. 109:72-80.

Franklin, J., and C. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA Forest Service, Gen. Tech. Rep. PNW-8. PNW Forest and Range Exp. Sta., Portland, Oregon.

Holmes, R. T., R. E. Bunney, Jr., and S. W. Pacala. 1979. Guild structure of the Hubbard Brook bird community: a multivariate approach. Ecology 60:512-520.

Huff, M. H. 1984. Post-fire succession in the Olympic Mountains, Washington: forest vegetation, fuels, and avifauna. University of Washington, Seattle, Washington. Dissertation.

Kendeigh, S. C., and B. J. Fawver. 1981. Breeding bird populations in the Great Smokey Mountains, Tennessee and North Carolina. Wilson Bull. 93:218-242.

MacMahon J., and D. Andersen. 1982. Subalpine forests: a world perspective with emphasis on western North America. Progr. Phys. Geogr. 6:368-425.

Maurer, B. A., and R. C. Whitmore. 1981. Foraging of five bird species in two forests with different vegetative structure. Wilson Bull. 93:478-490.

Mewaldt, R. 1956. Nesting behavior of the Clark's nutcracker. Condor 58:3-23.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. J. Wiley and Sons, Inc., New York.

Odum, E. P. 1950. Bird populations of the Highlands (North Carolina) Plateau in relation to plant succession and avian invasion. Ecology 31:587-605.

Rabenold, K. N. 1978. Foraging strategies, diversity, and seasonality in bird communities of Appalachian spruce-fir forests. Ecol. Monogr. 48:397-424.

Reynolds, R., J. Scott, and R. Nussbaum. 1980. A variable circular plot method for estimating bird numbers. Condor 82:309-313.

Sabo, S. 1980. Niche and habitat relations in subalpine bird communities of the White Mountains of New Hampshire. Ecol. Monog. 50:241-259.

Sabo, S., and R. Holmes. 1983. Foraging niches and the structure of forest bird communities in contrasting montane habitats. Condor 85:121-138.

Smith, K. 1980. Nongame birds of the Rocky Mountain spruce-fir forests and their management. Pp. 258-259. *In* R. Degraaf (Tech. Coordinator) Workshop proceedings management of western forests and grasslands for nongame birds. U.S.D.A. Forest Service Gen. Rept. INT-86.

_____. 1982. Drought-induced changes in avian community structure along a montane sere. Ecology 63:952-961.

Smith, K., and J. MacMahon. 1981. Bird communities along a montane sere: community structure and energetics. Auk 98:8-28.

Tomback, D. 1977. Foraging strategies of Clark's nutcracker. Living Bird 16:123-161.

Wiens, J. 1975. Avian communities, energetics, and functions in coniferous forest habitats. *In* D. Smith (Tech Coordinator) Proceedings of the symposium on management of forest and range habitats for nongame birds. U.S.D.A., Forest Service Gen. Tech. Rept. WO-1. Pp. 226-265.

Received 21 March 1986
Accepted for publication 3 October 1986

Martin H. Posey
Oregon Institute of Marine Biology, Charleston, Oregon 97420

Effects of Lowered Salinity on Activity of the Ghost Shrimp *Callianassa californiensis*

Abstract

Salinity variations can be an important determinant of activity and survival for intertidal and estuarine organisms. Many of these species must withstand abrupt, short-term salinity fluctuations such as might occur during a tidal cycle or after heavy rains. Animals exhibit a variety of behavioral responses to these short-term changes, in many cases limiting their contact with the overlying water. Decreased winter activity of the ghost shrimp, *Callianassa californiensis,* was considered one possible response to changing salinity. Activity of ghost shrimp was observed at various salinities in an artificial mudflat aquarium to determine if decreased salinity levels lowered winter activity. Active movement was positively related to salinity. However, this behavior showed considerable variability in duration. These results are consistent with the responses of other crustaceans, as well as bivalves and polychaetes, to acute changes in salt concentrations and emphasize the potential importance of salinity in modifying the behavior patterns of estuarine organisms.

Introduction

Salinity fluctuations can affect both survival and behavior of estuarine and intertidal organisms. Recent studies have indicated that abrupt salinity stress, such as might occur during a tidal cycle or after a storm, may elicit similar behavioral responses from different invertebrate groups. Many of these are short-term responses, often involving reduced activity, that apparently limit contact between the animal and potentially unfavorable water conditions (Davenport 1976, 1979; Davenport *et al.* 1980; Djangmah *et al.* 1979). Such reactions are adaptive in an environment where salinity stress is acute. The following study was undertaken to determine whether salinity fluctuations influence winter activity of an estuarine ghost shrimp, *Callianassa californiensis.*

The ghost shrimp is a common inhabitant of intertidal sandflats from Alaska to Baja California (MacGinitie 1934). This active burrower continually disrupts near-surface sediments, strongly affecting the distributions of other organisms (Bird 1982, Brenchley 1978, Posey 1986, Ronan 1975). It lives within a branched burrow system, usually with two or more holes and several blind tunnels, that extends up to 50 cm into the substrate (Swinbanks and Murray 1981). The ghost shrimp, which must maintain at least intermittent contact with the overlying surface water to obtain oxygen (Torres *et al.* 1977), spends a significant proportion of time in near-surface sediments while feeding (MacGinitie 1934). This behavior makes the species susceptible to both acute and long-term changes in water salinity. Seasonal observations of burrow hole densities indicate that *C. californiensis* produce 50% fewer holes per individual during winter months than in summer (Posey 1985). Because burrow holes must be actively maintained (Thompson and Pritchard 1969), the seasonal decline in hole density may be associated with decreased ghost shrimp activity.

Methods

To provide background information on general behavior patterns, *Callianassa californiensis* were observed in a 190 l sediment-filled aquarium. The aquarium had a flow-through water system and was filled to a depth of 0.4 m with sifted sand from a moderately dense ghost shrimp bed. The substrate surface retained a light color, indicating oxygenation throughout the study.

Because of the difficulty in observing and timing behaviors of shrimp burrowed in sediment, *C. californiensis* behavior was quantified in an outdoor aquarium that simulated burrow conditions (Hoffman 1981). The aquarium was divided into two compartments, each with three suspended U-shaped clear plastic tubes (2 cm inner diameter). One compartment received seawater (30-33‰ salt during the study) pumped from the mouth of Coos Bay, Oregon. The salinity of water entering the other half was varied in stages from 33‰ to 10‰. Since ghost shrimp normally receive light only from the surface, the aquarium

was skirted with black plastic to reduce light exposure to the plastic tubes.

Ghost shrimp were collected from a sandflat near Charleston, Oregon, and transferred directly from the field to the observation aquarium. One shrimp was added to each of the plastic tubes. Salinity in the experimental compartment was changed gradually and the shrimp were allowed to acclimate for 3-4 days before observations began (Thompson and Pritchard 1969). The division of the aquarium allowed different individuals to be observed simultaneously at ambient (30-33 ‰) and lowered salinities to reduce confounding effects from other environmental factors. Each shrimp was observed for a single 20-minute period at one salinity level. Over the entire study, observations were made at 13 salinity levels: 33, 30, 29, 27, 26, 25, 22, 20, 17, 15, 12, 11, and 10‰.

Linear regression, blocking for time of observation (morning, midday, or evening), was used to examine the effect of decreasing salinity on the time ghost shrimp spent actively moving within the tubes. The data were recorded as percentages of the total observation time and were arc sine transformed before analysis (Sokal and Rohlf 1981). The regression was calculated using the General Linear Models Procedure of the Statistical Analysis System (Ray 1982).

Field measurements of water salinity were made in a dense ghost shrimp bed near the Oregon Institute of Marine Biology at low tide during February and March 1983, periods of high freshwater input into Coos Bay, and in July 1983, a period of relatively low freshwater input. Salinity was recorded from near-surface channel water (20 cm depth), within *Callianassa californiensis* burrows, and from interstitial water. To sample interstitial water, a 15 cm pit was dug at low tide and the water that pooled in the bottom was collected. The pits were not used if there was apparent contamination of water from burrows or the surface. Water from *C. californiensis* burrows was obtained with a pipette. All field and laboratory salinities were measured with an American Optical no. 10419 refractometer.

Results

Callianassa californiensis showed a varied repertoire of behaviors within the sediment-filled aquarium. These behaviors fell into five general categories: burrowing; cleaning; pleopod movement (ventilation); aggressive interactions between shrimp; and sedentary behavior (lack of any detectable movement). Most active movement was involved with burrowing. This included the excavation of sediment, packing of the burrow walls using the walking legs, and transport of particles (often to the substrate surface). Feeding, which often involved sifting of sediment using the maxillipeds, could not be readily distinguished from nonfeeding burrowing activities.

Most of the patterns seen within the sediment-filled tank were also observed within artificial burrows. Burrowing was not possible within plastic tubes; however, shrimp spent a considerable amount of time moving, often carrying accumulated sediment. Since ghost shrimp often tried to carry sediment or "pack" the tube walls while moving, it is likely that this behavior is related to burrowing observed in the sediment-filled aquarium. Active movement was the most frequently observed behavioral pattern at 30‰ salt, comprising an average of 47% of each observation period. Cleaning and pleopod beating, which sometimes occurred concurrently with movement, were observed with about half this frequency. Shrimp were inactive for over 27% of an average observation period.

Measurements of *Callianassa californiensis* burrow water salinities, as well as those of the interstitial water and channel water, indicated that ghost shrimp are subject to reduced salinities during the winter months. Interstitial and burrow salinities remained almost identical, varying from 17‰ in February to 31‰ salt in July. Low-tide surface water had generally lower salinities, ranging from 4‰ in February to 27‰ salt in July.

When *Callianassa californiensis* in the artificial burrows were exposed to 8-9‰ salt concentration, 75-100% died. This result agrees closely with that of Thompson and Pritchard (1969). No salinity related mortality occurred at 10‰ salt and only observations at this or higher concentrations were used to examine the effects of salinity on behavior.

A trend toward decreased activity was observed with lower salinities (Figure 1). However, this pattern is not significant at the 0.05 level ($p < .066$), much of the deviation being due to high activity at 15‰. While the data for activity

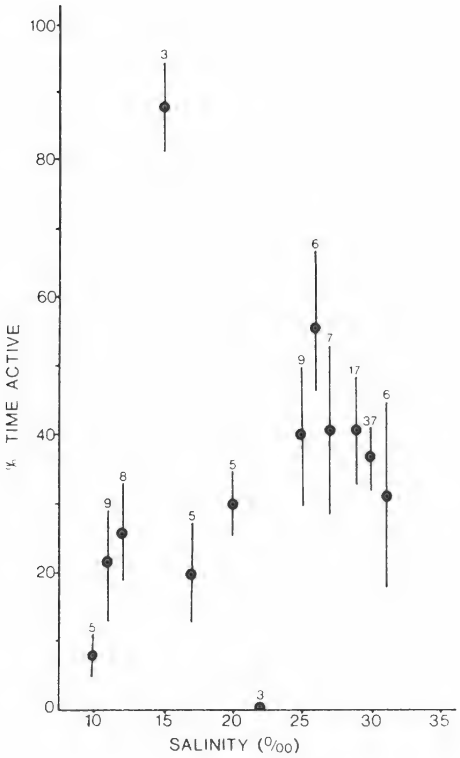

Figure 1. Relationship between salinity and active movement of ghost shrimp within artificial burrows. Bars represent 95% confidence intervals and numbers above bars show sample size.

at other salinity levels represent observations made over several days, those at 15‰ all stem from a single mid-afternoon session. Since the tank was located outdoors, unusual conditions on that day (such as extreme temperature, light, etc.) may have contributed to the higher activity. Dixon's test for extreme observations (Snedecor and Cochran 1980) indicates that this mean is an outlier when compared to the other data (ratio = 0.593; $p < .05$). Recalculation of the regression excluding these values indicates a significant decline in activity with reduced salinity ($F = 6.15$; $p < .015$; $r = .35$).

Because of the large size of the observation aquarium, observations of salinity/behavior relationships were made outdoors. This presents problems in the interpretation of results due to confounding effects from other environmental factors. Temperature, in particular, is known to influence activity. The experimental design was meant to control for the influence of factors other than salinity by simultaneously observing different ghost shrimp at full-strength seawater and at reduced salinities. The statistical analysis blocked for diurnal variations in activity that may be related to fluctuations in light. The effects of temperature on movement was also indirectly estimated. Water temperature was recorded on a daily basis near the intake for the seawater system that supplied the observation aquarium. The very short residence time of water within this seawater system meant that temperatures at the intake point were close to those entering the observation aquarium. Water temperatures for the days on which observations were made, along with maximum and minimum air temperatures recorded at the North Bend airport (approximately 5 miles from Charleston, Oregon), were tested against shrimp activity using multiple linear regression (Ray 1982). Only maximum daily air temperature showed a significant relationship, with activity decreasing slightly with increasing temperature ($r = 0.32$; $F = 8.59$; $p < .005$). However, the percentage of observations made on warm days was approximately equal for high and low salinity levels. Thirty one percent of the observations for ≥ 29‰ were made at temperatures equalling or exceeding 68° F, while 29% of those observations for salinities less than 26‰ were made at these same temperatures. Thus, a decline in movement with decreasing salinity does not appear to be due to confounding temperature effects.

Discussion

The results of this study suggest that salinity may affect activity of *Callianassa californiensis.* Many short-term responses of invertebrates involve a cessation of activity when exposed to rapid declines in salinity. These include reduced feeding activity followed by valve closure in barnacles (Davenport 1976), withdrawal of the hermit crab, *Pagurus bernhardus* L., into its shell (Davenport *et al.* 1980) and decreased activity of the polychaete, *Arenicola marina* L., within its burrow (Shumway and Davenport 1977). The similarity of the salinity of interstitial water and that within *Callianassa californiensis* burrows, even during times of low surface water salinity,

indicates that ghost shrimp also may employ a short-term response to reduce contact with the overlying water. Reduced activity, with an associated decline in burrow hole maintenance, would have the effect of decreasing water exchange with the surface.

As is apparent from the large variance in the time spent actively moving, salinity is only one of several factors influencing this behavior. On a seasonal scale, temperature may be more important in causing variations in activity of ghost shrimp. However, determination of even small effects, such as observed between active movement and salinity for the ghost shrimp, will contribute to an understanding of the interactions between organisms and their environment.

Acknowledgments

I wish to thank Steven Holmes and Susan Thorpe for their help and encouragement in this study. The study was aided by numerous discussions with Robert Graham, Marshall Pregnall, and Peter Frank.

Literature Cited

Bird, E. W. 1982. Population dynamics of the thalassinidean shrimps and their community effects through sediment modification, University of Maryland, College Park. Ph.D. Dissertation.

Brenchley, G. A. 1978. On the regulation of marine infaunal assemblages at the morphological level: a study of the interactions between sediment stabilizers, destabilizers, and their sedimentary environment. The Johns Hopkins University, Baltimore, Ph.D. Dissertation.

Davenport, J. 1976. A comparative study of the behavior of some balanomorph barnacles exposed to fluctuating seawater concentrations. J. Mar. Biol. Assoc. U.K. 56:889-907.

_____. 1979. The isolation response of mussels (*Mytilus edulis* L.) exposed to falling seawater concentrations. J. Mar. Biol. Assoc. U.K. 59:123-132.

Davenport, J., P. M. C. F. Busschots, and D. F. Cawthorne. 1980. The influence of salinity on behavior and oxygen uptake of the hermit crab *Pagurus bernhardus* L. J. Mar. Biol. Assoc. U.K. 60:127-134.

Djangmah, J. S., S. E. Shumway, and J. Davenport. 1979. The effects of fluctuating salinity on the behavior of the West African blood clam *Anodara senilis* and on the osmotic pressure and ionic concentration of the haemolymph. Mar. Biol. 50:209-213.

Hoffman, C. J. 1981. Associations between the arrow goby, *Clevelandia ios* (Jordan and Gilbert) and the ghost shrimp *Callianassa californiensis* Dana in natural and artificial burrows. Pac. Sci. 35:211-216.

MacGinitie, G. E. 1934. The natural history of *Callianassa californiensis* Dana. Amer. Midl. Nat. 15:166-175.

Posey, M. H. 1985. The effects upon the macrofaunal community of a dominant burrowing deposit feeder, *Callianassa californiensis,* and the role of predation in determining its intertidal distribution. University of Oregon, Eugene. Ph.D. Dissertation.

_____. 1986. Changes in a benthic community associated with dense beds of a burrowing deposit feeder, *Callianassa californiensis.* Mar. Ecol. Prog. Ser. 31:15-22.

Ray, A. A. (ed.) 1982. SAS user's guide, statistics, 1982 edn. SAS Institute, Cary, North Carolina.

Ronan, T. E. 1975. Structural and paleo-ecological aspects of a modern marine soft-sediment community: an experimental field study. University of California, Davis. Ph.D. Dissertation.

Shumway, S. E., and J. Davenport. 1977. Some aspects of the physiology of *Arenicola marina* (Polychaeta) exposed to fluctuating salinities. J. Mar. Biol. Assoc. U.K. 57:907-924.

Snedecor, G. W., and W. G. Cochran. 1980. Statistical methods. The Iowa State University Press, Ames, Iowa.

Sokal, R. R., and E. F. Rohlf. 1981. Biometry. W. H. Freeman, San Francisco.

Swinbanks, D. D., and J. W. Murray. 1981. Biosedimentological zonation of Boundary Bay tidal flats, Fraser River delta, British Columbia. Sedimentology 28:201-237.

Thompson, L. C., and A. W. Pritchard. 1969. Osmoregulatory capacities of *Callianassa* and *Upogebia* (Crustacea: Thalassinidea). Biol. Bull. 136:114-129.

Torres, J. J., D. L. Gluck, and J. J. Childress. 1977. Activity and physiological significance of the pleopods in the respiration of *Callianassa californiensis* (Dana) (Crustacea: Thalassinidea). Biol. Bull. 152:134-146.

Received 11 August 1986
Accepted for publication 6 February 1987

Paul S. Doescher, Lee E. Eddleman and **Milda R. Vaitkus**[1]
Department of Rangeland Resources, Oregon State University, Corvallis, Oregon 97331

Evaluation of Soil Nutrients, pH, and Organic Matter in Rangelands Dominated by Western Juniper[2]

Abstract

Establishment of western juniper (*Juniperus occidentalis* Hook) in sagebrush-steppe of central Oregon appears to have affected the distribution of total N, organic matter, Ca, K, and pH. Compared to interspace soils and soils under juvenile trees, soil Ca, K, and pH were significantly higher under mature trees. Highest concentrations of total N and organic matter were found in upper soil layers under juvenile canopies. Thus, invasion of western juniper changes mineral cycling in microenvironments beneath the canopy. Further, these changes occur in such a way as to apparently enhance the competitiveness of western juniper with other herbaceous vegetation.

Introduction

Over the past 100 years, land management has influenced the composition and productivity of plant communities in central Oregon. During this period, western juniper (*Juniperus occidentalis*) has invaded rangelands previously supporting a more floristically diverse sagebrush-grassland (Caraher 1978). Although understory production of herbaceous and suffrutescent plants has apparently declined on these areas (Bedell and Bunch 1978), the mechanisms by which western juniper impacts associated vegetation has not been assessed. Alterations of microsites by recently established western juniper, as shown for other woody species (Doescher *et al.* 1984, Parker and Muller 1982, Barth 1980, Brotherson and Osayande 1980), may enhance the competitive ability of this species and provide new niches for understory species (Tiedemann and Klemmedson 1973b, Charley and West 1975).

The purpose of this study was to examine spatial variability in soil constituents on an area invaded by western juniper of different age classes. Loss of understory production following juniper invasion suggests a modification of microsite characteristics. We felt that changes in nutrient distribution under canopies of western juniper may be a significant factor contributing to the progressive site dominance of this species and the decline of associated plant species.

Study Area

The study site is located on a gentle northwest-facing slope at an elevation of 1300 meters. Soils of the area are classified as frigid Pachic Argixerolls and are approximately 60 cm in depth to weathered basalt. Cobbles increase with depth, reaching approximately 30% in the lower 30 cm of the profile. Basalt rock beneath is covered with soft $CaCO_3$ capping. In recent years, the area has been used for winter and early spring grazing by cattle.

Samples were collected in the Fall of 1982 from an area southeast of Prineville in Crook County, Oregon. Precipitation was collected in rain gauges and ranged between 300-350 mm annually.

Western juniper occurs as an almost continuous woodland on the study site. A single 0.2 ha block sampled adjacent to this study area contained 76 individual trees, 19 of which were less than 1 meter tall, and a tree canopy cover of 40% (Vaitkus 1986). The oldest tree established in 1895. Most (65%) of the trees (over 1 meter tall) established between 1900 and 1920, and have an average age of 63 years. Largest trees are 12-14 meters in height, with a crown radius of approximately 3 meters.

Understory vegetation is dominated by mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana*), Idaho fescue (*Festuca idahoensis* Elmer), bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. and Smith) and Sandberg bluegrass (*Poa sandbergii* Vasey). Low sage (*Artemisia arbuscula* Nutt.), squirreltail (*Sitanion hystrix* (Nutt.) Smith), downy brome (*Bromus*

[1]Present address: Department of Soil Science, Oregon State University, Corvallis, OR 97331
[2]This article is submitted as Technical Paper No. 7708, Oregon Agricultural Experiment Station, Corvallis.

tectorum L.), tailcup lupine (*Lupinus caudatus* Kell), and milkvetch (*Astragalus reventus* Gray) are commonly found throughout the area.

Juniper roots are a conspicuous feature of the surface soils of the area. These roots are characteristically dark red in color and appear to diminish in areas between trees. A conspicuous root mat, about 5 cm thick, extends outward from the bole of the tree approximately 2/3 the distance to the canopy edge of larger trees. No root mat is observed beneath small and intermediate sized trees (<8 meters).

Materials and Methods

To examine spatial relationships of soil nutrients, pH, and organic matter, the soil surface was stratified into four zones. These zones were selected to represent a horizontal vegetation gradient away from the bole of individual juniper trees.

The first zone was an area adjacent to the bole of large, mature junipers (>80 years old). Individual trees were between 12 and 14 meters tall and had a canopy radius between 2.0 to 3.0 meters. This zone was either devoid of other vegetation or dominated by annual grasses such as downy brome. This zone was designated the MB zone because it occurred near the bole of mature trees.

The second zone was 1/2 to 2/3 the distance from the bole of large junipers toward the canopy edge. The vegetation of this zone was dominated by high seral perennial grasses, such as Idaho fescue and bluebunch wheatgrass. This zone was designated the MG zone because it occurred under the canopy of mature trees in a zone dominated by perennial grasses.

The third zone was located in the interspace areas between mature junipers and was characterized by considerable bare soil and small Sandberg bluegrass plants. No noticeable litter accumulation was evident in this zone which was designated the I zone because it occurred in the interspaces between trees.

The fourth zone was adjacent to the bole of small juvenile junipers (<40 years old). Individual trees were 2-3 meters tall and had a canopy radius of 0.75-1.5 meters. High seral perennial grasses such as Idaho fescue and bluebunch wheatgrass dominated this area. It was assumed that this zone reflected initial stages of juniper establishment and would provide a comparison of temporal changes in soil constituents relative to mature trees. Samples were removed from soils directly below the perennial grasses. This zone was designated the J zone because of its location under juvenile trees.

Zones associated with five large and five juvenile, randomly selected western juniper trees were sampled. Within each zone, surface litter was removed, pits were excavated, and mineral soil collected at depths of approximately 0-8 cm, 8-16 cm and 16-24 cm. These depths were selected to ascertain the presence of vertical chemical patterns in the zone of greatest root volume. Five soil samples at each depth/zone combination were extracted (Brotherson and Osayande 1980). Soils were sieved through a 4 mm screen, thoroughly mixed, and obvious root material and organic debris removed before analysis (Charley and West 1975).

Soil analysis was performed at the Oregon State University Soil Testing Laboratory. Total N was determined using the Micro-Kjeldahl method (Bremner and Edwards 1965); OM was estimated utilizing the wet oxidation-titration method of Walkley and Black (1934); P was determined by the sodium bicarbonate method of Olsen and Dean (1965); Ca, Mg, and Na were determined by the ammonium acetate method of Peech *et al.* (1947); K was determined by a modification of the technique used by Pratt (1965); and pH was measured using a 1:2 soil:water ratio and a glass electrode (Jackson 1958).

Analysis of variance with a split-plot design was used to test significant differences ($\alpha = 0.05$). Zones were analyzed as main plots and soil sampling depths were analyzed as subplots. Where interactions existed, two-way interaction means were separated using a protected least significant differences (LSD) procedure. Where no interactions were detected, LSD was used to separate main-effect means (Steel and Torrie 1980).

Results

Total N, Ca, K, pH, and OM levels were significantly different between zones and between depths within zones. These soil constituents also exhibited a significant zone x depth interaction. The following relationships were noted:

1. Concentrations of Ca were greatest in surface soils (0-8 cm) near the bole of large juniper trees (MB zone) and declined with distance from the bole in the MG and I zones (Table 1). There were no significant differences in concentration with distance from the bole at the 16-24 cm soil depth. Calcium concentrations near the bole of juvenile trees (J zone) were similar to those in the MG and I zones, but were always lower than in the MB zone.

Presence of juniper canopies strongly influenced surface concentration of Ca. Ca concentrations in the MB and MG zones at the 0-8 cm sampling depth were greater than at the 8-16 cm and 16-24 cm depths. In the J zone, Ca concentrations at the 0-8 cm depth were greater than at the 8-16 cm depth, but not different from the 16-24 cm depth. Calcium concentrations showed no depth related patterns in the I zone.

2. Highest levels of organic matter in the mineral soil were found predominately in the zones beneath juniper canopies (Table 2). Levels of organic matter were highest in the 0-8 cm depth under the J zone compared to the other zones. Next greatest surface levels were found near the boles of large juniper trees (MB zone) and became progressively lower in the MG and I zones. Results at the 8-16 cm depth showed no clear patterns. Differences between zones were nonsignificant at the 16-24 cm sampling depth.

Soil depth also significantly influenced OM content of the soil. Organic matter levels were highest at the 0-8 cm depth in all zones and declined with increasing soil depth.

3. Total N levels of surface soils were greater in the J zone than those found in the MB, MG and I zones (Table 3). No differences in surface levels of total N were detected between the MB and MG zones and the MB and I zones. At the 8-16 and 16-24 cm sampling depths, no differences in levels of total N were found among zones.

Total N levels showed depth dependent patterns. Highest total N levels were found near the surface in all zones, and were lowest at the deepest sampling depths.

4. Concentrations of K were greatest in surface soils in the MB and MG zones and least in the I zone (Table 4). Surface concentrations of K in the J zone did not differ from either the MG or I zones, although concentrations in the MG zone were greater than in the I zone. The pattern of K concentration became less distinct with depth.

In the MB, MG and J zones, concentrations of K at 0-8 cm were higher than those found at the 8-16 cm and 16-24 cm sampling depths. Potassium concentrations did not differ with depth in the I zone.

TABLE 1. Mean Ca concentration (cmol (p^+) Kg^{-1}) at three depths in a *Juniperus occidentalis* woodland.

Soil Depth	Zone			
cm	MB	MG	I	J
0-8	19.8^{Aa*}	16.1^{Ba}	12.4^{Ca}	14.56^{Ba}
8-16	15.7^{Ab}	14.2^{ABb}	12.6^{BCa}	12.34^{Cb}
16-24	14.9^{Ab}	14.3^{ABb}	13.20^{ABa}	12.86^{Bab}

EMS (zone comparison) = 1.38
EMS (depth comparison) = 1.86
*Identical capital letters indicate nonsignificant differences ($\alpha = .05$) among MB, MG, I, and J soil zones at a particular soil depth. Identical lower case letters denote nonsignificant differences among soil depths within MB, MG, I, and J zones.

TABLE 2. Mean OM concentrations (% D.W.) at three depths in a *Juniperus occidentalis* woodland.

Soil Depth	Zone			
cm	MB	MG	I	J
0-8	5.9^{Aa*}	5.1^{Ba}	4.2^{Ca}	6.8^{Da}
8-16	4.3^{ABb}	3.7^{Ab}	3.8^{Aab}	4.5^{Bb}
16-24	3.6^{Ac}	3.5^{Ab}	3.4^{Ab}	3.9^{Ac}

EMS (zone comparison) = .24
EMS (depth comparison) = .18
*Identical capital letters indicate nonsignificant differences ($\alpha = .05$) among MB, MG, I, and J soil zones at a particular soil depth. Identical lower case letters denote nonsignificant differences among soil depths within MB, MG, I, and J zones.

TABLE 3. Mean total N (% D.W.) concentrations at three depths in a *Juniperus occidentalis* woodland.

Soil Depth	Zone			
cm	MB	MG	I	J
0-8	$.17^{ABa}$	$.19^{Aa}$	$.15^{Ba}$	$.28^{Ca}$
8-16	$.14^{Ab}$	$.14^{Ab}$	$.13^{Aab}$	$.16^{Ab}$
16-24	$.13^{Ab}$	$.13^{Ab}$	$.12^{Ab}$	$.14^{Ab}$

EMS (zone comparison) = .0006
EMS (depth comparison) = .0005
*Identical capital letters indicate nonsignificant differences ($\alpha = .05$) among MB, MG, I, and J soil zones at a particular soil depth. Identical lower case letters denote nonsignificant differences among soil depths within MB, MG, I, and J zones.

Magnesium, Na, P and pH did not exhibit a zone x depth interaction. Separation of main effect means for these constituents revealed the following relationships:

1. Concentrations of Mg and Na increased with soil depth (Table 5), but did not differ among zones.

2. Concentrations of P decreased with soil depth (Table 5), but did not differ among zones.

3. Highest pH values were found in the MB zone (Table 6). Intermediate pH values were detected in the MG zone while lowest levels were found in the I and J zones. Levels of pH in the J zone did not differ from the I zone. No differences in pH were detected with increasing soil depth.

Discussion

Examination of soil constituents in a western juniper community provided insight into possible changes in mineral cycling brought about by invasion of this species. Soil constituents such as total N, total S, K, and organic matter have been found to accumulate at the soil surface beneath non-halophytic shrubs (Tiedemann and Klemmedson 1973a, Charley and West 1975, Doescher *et al.* 1984). Our findings, however, indicated several unique patterns of total N and Ca accumulations associated with establishment of western juniper.

A strong accumulation of total N was detected at the 0-8 cm depth in the J zone in comparison to the MB, MG and I zones. The reason for this high N accumulation in the surface horizon under juvenile trees (J zone) is not entirely clear. The enhancement may be related to the young age of the junipers and sampling of soils dominated by high seral perennial grasses. Accumulation of grass litter and the absence of tree litter may result in higher total N levels in soils of the J zone. In contrast, litter, especially under large junipers, may be slow to decompose and not allow for the accumulation of total N in surface soils. Visual observation of the detritus at the bottom of the litter mat in both the MB and MG zones revealed recognizable plant material. Juniper foliage as well as bunchgrass tillers were found essentially intact. Feeder roots of juniper at the soil/litter interface may serve as efficient collectors of mineralized nitrogen. Nitrogen accumulations in ecosystems dominated by western juniper may actually be associated with litter and/or biomass of juniper trees.

TABLE 4. Mean K concentration (mg Kg^{-1}) at three depths in a *Juniperus occidentalis* woodland.

Soil Depth	Zone			
cm	MB	MG	I	J
0-8	777.4^{Aa}	685.6^{ABa}	481.8^{Ca}	572.4^{BCa}
8-16	662.0^{Ab}	589.0^{ABb}	490.8^{Ba}	509.2^{ABab}
16-24	637.4^{Ab}	561.4^{ABb}	497.8^{ABa}	473.6^{Bb}

EMS (zone comparison) = 20055.8
EMS (depth comparison) = 2438.2
*Identical capital letters indicate nonsignificant differences ($\alpha = .05$) among MB, MG, I, and J soil zones at a particular soil depth. Identical lower case letters denote nonsignificant differences among soil depths within MB, MG, I, and J zones.

TABLE 5. Main effect means for concentrations of Mg (cmol (p^+) Kg^{-1}), Na (cmol (p^+ Kg^{-1}), and P (mg Kg^{-1}) at soil depths of 0-8 cm, 8-16 cm, and 16-24 cm. No differences were detected between zones.

	Soil Chemical		
Soil Depth	Mg	Na	P
0-8 cm	6.7^{a*}	$.17^{a}$	15.9^{a}
8-16 cm	7.10^{a}	$.17^{a}$	14.5^{ab}
16-24 cm	7.7^{b}	$.19^{b}$	13.5^{b}

EMS (Mg) = .45
EMS (Na) = .0007
EMS (P) = 7.94
*Identical letters indicate nonsignificant differences ($\alpha = .05$) at a particular soil depth.

TABLE 6. Main effect means for levels of soil pH between MB, MG, I, and J. No differences were detected between soil depths.

	Zone			
	MB	MG	I	J
pH levels	6.6^{A*}	6.4^{B}	6.3^{C}	6.3^{C}

(EMS = .0087)
*Identical letters indicate nonsignificant differences ($\alpha = .05$) at a particular soil depth.

Increased levels of Ca beneath juniper canopies may result from two processes: 1) mineral washing in stem flow (Young *et al.* 1984); and/or 2) decomposition of needles which are probably high in Ca, as has been found for

Juniperus scopulorum (Hart and Parent 1974). These changes could enhance the competitiveness of western juniper by altering soil chemical dynamics in favor of western juniper. For instance, increased Ca concentrations coupled with alterations in soil pH under canopy soils may affect growth of herbaceous vegetation. Observations of plant species under canopies of large western junipers have shown distinct spatial segregation with distance from the bole of individual trees (Vaitkus 1986). These understory patterns likely result from changes in soil nutrients under western juniper, as well as other microenvironmental alterations resulting from establishment of this species.

Conclusions

Distribution of soil constituents in arid regions provides insight into functional roles vegetation has on ecosystem processes. Results support hypotheses proposed by Archer *et al.* (1985). which state that, in arid environments invaded by shrubs (in their case—*Prosopis glandulosa* Torr.), autogenic alterations induced by the shrub alter microsite conditions to the benefit of woody vegetation. For western juniper, redistribution of soil constituents may be one such autogenic process which enhances its competitiveness.

Based upon comparisons between four sampling zones, our evidence suggests a potential decrease in total soil N under juniper canopies during the time between establishment and maturity. Redistribution of N pools may also have occurred. In addition, alterations in soil nutrients, such as Ca, may promote the persistence of western juniper and the reduction in understory vegetation. How these factors influence plant succession and competitive interactions between western juniper and herbaceous species will be addressed in future research.

Literature Cited

Archer, S., C. J. Scifres, and W. H. Blackburn. 1985. Autogenic succession in *Prosopis*-mixed shrub stands of south Texas. Abstracts 38th Annual Meeting, Society for Range Management.

Barth, R. C. 1980. Influence of pinyon pine trees on soil chemical and physical properties. Soil Sci. Soc. Amer. J. 44:112-114.

Bedell, T. E., and T. R. Bunch. 1978. Effects of western juniper on grass production and livestock grazing management. *In:* Martin J. E., J. E. Dealy, and D. L. Larcher (eds.) Proc. Western Juniper Ecology and Management Workshop. U.S. Forest Service, General Tech. Rep. PNW-74.

Bremner, J. M., and A. P. Edwards. 1965. Determination and isotope-ratio analysis of different forms of nitrogen in the soil. Soil Sci. Soc. Amer. Proc. 29:504-507.

Brotherson, J. D., and S. T. Osayande. 1980. Mineral concentrations in true mountain mahogany and Utah juniper, and in associated soils. J. Range Manage. 22:182-185.

Caraher, D. L. 1978. The spread of western juniper in central Oregon. *In:* Martin, J. E., J. E. Dealy, and D. L. Larcher (eds.) Proc. Western Juniper Ecology and Management Workshop. U.S. Forest Service General Tech. Rep. PNW-74.

Charley, J. L., and N. E. West. 1975. Plant induced soil chemical patterns in some desert shrub-dominated ecosystems in Utah. J. Ecol. 63:945-964.

Doescher. P. S., R. F. Miller, and A. H. Winward. 1984. Soil chemical patterns under eastern Oregon Plant communities dominated by big sagebrush. Soil Sci. Soc. Amer. J. 48:659-663.

Hart, G. E., and D. R. Parent. 1974. Chemistry of throughfall under Douglas-fir and Rocky Mountain juniper. Amer. Midl. Nat. 92:191-201.

Jackson, M. L. 1958. Soil chemical analysis. Prentice-Hall, Englewood Cliffs, New Jersey.

Olsen, S. R., and L. A. Dean. 1965. Phosphorous. *In:* C. A. Black *et al.* (ed.) Methods of soil analysis, part 2. Agronomy 9:1035-1048. Am. Soc. of Agron., Madison, WI.

Parker, V. T., and C. H. Muller. 1982. Vegetational and environmental changes beneath isolated live oak trees (*Quercus agrifolia*) in a California annual grassland. Amer. Midl. Nat. 107:69-81.

Peech, M. L., T. Alexander, L. A. Dean, and F. F. Reed. 1947. Methods of soil analysis for fertility investigations. USDA Circ. 757. U.S. Government Printing Office, Washington, D.C.

Pratt, P. G. 1965. Potassium. In C. A. Black *et al.* (ed.) Methods of soil analysis, part 2. Agronomy 9:1022-1030. Amer. Soc. of Agron., Madison, WI.

Steel, R. G. D., and J. H. Torrie. 1980. Principles and procedures of statistics, 2nd ed. McGraw-Hill Book Co., Inc., New York.

Tiedemann, A. R., and J. O. Klemmedson. 1973a. Effect of mesquite on physical and chemical properties of the soil. J. Range Manage. 26:27-29.

_____. 1973b. Nutrient availability in desert grassland soils under mesquite (*Prosopis juliflora*) trees and adjacent open areas. Soil Sci. Soc. Amer. Proc. 37:107-111.

Vaitkus, M. R. 1986. Effect of western juniper on understory herbage production in central Oregon. MS Thesis, Oregon State University, Corvallis.

Walkley, A., and I. A. Black. 1934. An examination of the Degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. Soil Sci. 37:29-38.

Young, J. A., R. A. Evans, and D. A. Easi. 1984. Stem flow on western juniper (*Juniperus occidentalis*) trees. Weed Sci. 32:320-327.

Received 3 June 1986
Accepted for publication 18 November 1986

P. B. Hamm and **E. M. Hansen,** Department of Botany and Plant Pathology
Oregon State University, Corvallis, OR 97331

Identification of *Phytophthora* spp. known to Attack Conifers in the Pacific Northwest

Abstract

Fungi belonging to the genus *Phytophthora* are some of the most destructive plant pathogens worldwide. Unlike most plant pathogens, members of this genus produce swimming zoospores that follow a gradient of root exudates to host tissue. In the Northwest, Phytophthora diseases are most damaging on crops in poorly drained or irrigated soils. Species are difficult to isolate and even more difficult to identify. Of the more than 50 *Phytophthora* species described worldwide, nine are associated with serious diseases on conifers grown in the Pacific Northwest. Physiological and morphological characteristics of these species are described which are particularly useful when identifying Pacific Northwest isolates. Methods for observing the fungi are provided along with a key to simplify species identification. The geographical range within the region and conifer hosts attacked are identified.

Introduction

Phytophthora spp. cause serious diseases in Pacific Northwest conifers. *Phytophthora lateralis* Tuck. & Milb. kills indigenous Port-Orford-cedar (*Chamaecyparis lawsoniana*) [A. Murr.] Parl. in the forests of southwestern Oregon and northern California (Roth *et al.* 1957, Zobel *et al.* 1985, Kliejunas and Adams 1981) and, along with *P. cinnamomi* Rands., is a fatal root pathogen of Port-Orford-cedar in ornamental plantings (Torgeson *et al.* 1954). Species that cause damage to a wide range of conifer seedlings in Oregon, Washington, and British columbia nurseries include *P. cryptogea* Peth. and Lef., *P. cactorum* (Leb. and Cohn.) Schr., *P. drechsleri* Tucker, two distinguishable groups of *P. megasperma* Drech. emend Hamm & Hansen, *P. pseudotsugae* Hamm & Hansen, and *P. cinnamomi* Rands (Hamm *et al.* 1985; Pratt *et al.* 1976, Hansen *et al.* 1980, Hamm and Hansen 1982a, 1982b, 1983; Kanaskie, pers. comm.). Recently *P. cambivora* was associated with root rot and stem cankers on Noble fir grown for Christmas trees (P. B. Hamm and G. A Chastagner, unpublished data).

In the past, *Phytophthora* spp. may have been overlooked as a cause of tree mortality because of difficulties in isolation, recognition, and identification of the pathogen. Recent advances in chemical control (Hamm *et al.* 1984) and information on the host preferences of these fungi can be useful in disease management, but only after the pathogens are properly identified. Because more than 50 species of *Phytophthora* are described worldwide (Waterhouse and Blackwell 1954; Waterhouse 1963, 1970; Newhook *et al.* 1978) a simplified key is needed for identifying those species that are specifically associated with Pacific Northwest conifers. By limiting the number of *Phytophthora* species included, a regional identification key (such as that published for the British Isles by Waterhouse and Blackwell [1954]) can use characteristics (usually physiological) specific to local isolates which could not be used in a worldwide key. This paper presents such a regional key for identifying *Phytophthora* species known to attack Pacific Northwest conifers.

Characteristics of *Phytophthora*

Oogonia and oospores

Phytophthora has a diploid life cycle. A single, spherical oospore is formed within an oogonium following attachment (fertilization) by a one or two-celled antheridium. The presence of oospores, location of antheridial attachment, the sizes of these structures, and whether the oogonial wall is smooth or ornamented are important features in distinguishing *Phytophthora* spp. Oospores may be formed by a single isolate (homothallic species) or only by mating two sexually different isolates (heterothallic species). Antheridia attach either around the oogonial stalk (amphigynous) or elsewhere on the oogonium (paragynous), sometimes adjacent to the stalk (Figure 1). Oospores are distinguished from similarly shaped chlamydospores by the presence of two walls—the external oogonial wall and an internal, often thicker wall around the oospore itself—and by the presence of antheridia.

Most homothallic species from Pacific Northwest conifers form oogonia on clarified V-8 agar after 1-3 weeks in the dark at room temperature. To prepare clarified V-8 agar: add 200 ml of V-8® juice to 1.5 g calcium carbonate, heat for 5 minutes in an autoclave, and then centrifuge for 15 minutes at 2,000 RPM. To each 200 ml of supernatant add 800 ml distilled water and 15 g of agar, then autoclave (Pratt and Mitchell 1973). If oogonia have not formed within 4 weeks, repeat the procedure with fresh agar. Repeated failure suggests a heterothallic species, which should be paired with known isolates of both mating types to confirm heterothallism.

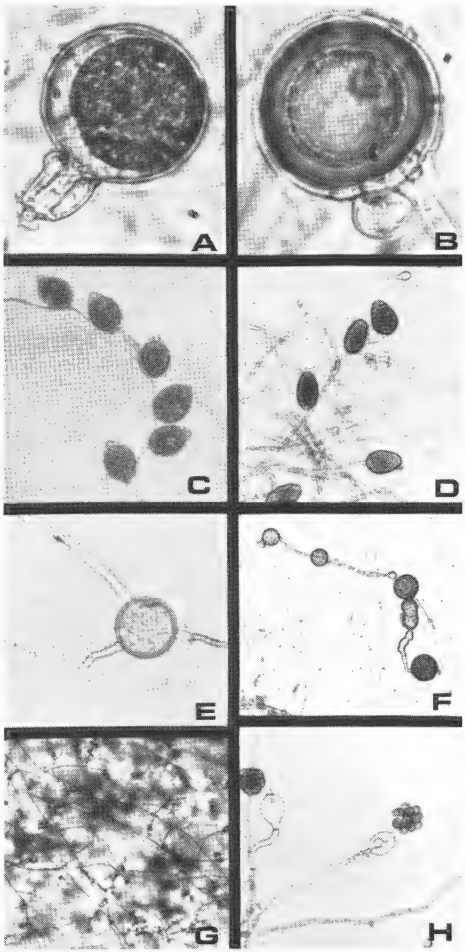

Figure 1. Oogonia, sporangia and chlamydospores characteristic of *Phytophthora*. (A) Oogonia containing oospores with amphigynous and (B) paragynous antheridia. (C) Sympodially born papillate sporangium. (D) Ovoid and ellipsoid sporangia. (E) Hyphal swelling. (F) Terminal and intercallary chlamydospores on one hypha. (G) Mycelia characteristic of *P. cinnamomi*. (H) *Pythium* sporangia with protoplasm differentiating into zoospores within vesicles.

Chlamydospores

Chlamydospores are spherical, relatively thick-walled, single-celled spores, formed by some species of *Phytophthora*, and presumably function as resting structures. They develop in clarified V-8 agar and can be either intercalary or terminal (Figure 1). They are delimited from subtending hyphae by septa, which also distinguish them from hyphal swellings which are not walled off. As mentioned previously, chlamydospores differ from oogonia by their lack of a double wall or of an antheridium.

Hyphal-swellings

Spherical, ellipsoid or irregular swellings may form terminally or intercalary on vegetative hyphae. In appearance hyphal swellings differ from oogonia by their lack of double walls and antheridia, and from chlamydospores by lack of septations.

Sporangia

The asexual zoospores of *Phytophthora* are produced within sporangia when colonies are in water or saturated soil. Sporangia generally are spherical, ovoid, obpyriform or ellipsoid in shape and are either papillate (i.e., having a terminal protrusion, Figure 1c) or non-papillate (Figure 1d). Sporangial shape and size vary with age and growth conditions so they should be observed when first formed. Zoospores of *Phytophthora* differentiate within the sporangia and are released fully formed directly into water. In contrast, zoospores of *Pythium,* a similar and closely related genus, do not form until the undifferentiated sporangial protoplasm has extruded into a vesicle attached to the sporangium (Figure 1H).

Usually sporangia are produced on colonies grown in pea broth (150 g of split peas in 1 L of distilled water, heated in an autoclave for three minutes, filtered through double cheesecloth,

then bottled and autoclaved for 15 minutes [Trione 1974]). Colonies are cultured in the dark for 3-5 days and then carefully and thoroughly rinsed with distilled water and flooded with soil extract water (SEW, equal amounts of soil and water mixed, left overnight at room temperature, and then filtered) for 8-12 hours in the dark to induce sporangia. Zoospores are often released during this period. Deciduous sporangia are detected by vigorously swirling flooded colonies. Deciduous (caducous) sporangia float free.

Identification to Genus

The relatively slow growth of *Phytophthora* spp. makes their isolation from the many other fungi of the root/soil environment difficult. The first challenge of identification is to separate *Phytophthora* from other fungi. Basically, all isolation procedures belong to two general categories: 1) baiting with seedlings or other plant tissues (Hamm and Hansen 1984, Linderman and Zeitoun 1977, McIntosh 1966, Ostrofsky *et al.* 1977, Roth pers. comm.); or 2) plating soil or infected tissue directly on selective media (Eckert and Tsao 1962, Pratt *et al.* 1976, Tsao and Ocana 1969). Fortunately the antibiotic Pimaricin (Delvicide 50% WP, GB Fermentation, Des Plaines, IL 60016) in all media prevents growth of most fungi except *Phytophthora* and *Pythium* (Eckert and Tsao, 1962). Another

Key to *Phytophthora* Species Attacking Conifers in the Pacific Northwest.

A_1 Zoospores liberated from vesicle attached to sporangium (Figure 1H) — *Pythium* spp

A_2 Zoospores liberated directly from sporangium. (Figures 1C and D) — *Phytophthora* spp. — B

B_1 Oogonia with predominantly (>50%) paragynous antheridia produced in single strain culture on clarified V-8 agar — C

C_1 Oogonia average >46 μm — *P. megasperma* — Group 2

C_2 Oogonia average <44 μm — D

D_1 Sporangia non-papillate and non-deciduous, ovoid or pear-shaped (length/width ratio usually large from 1.4:1.0 to 1.6:1.0) — *P. megasperma* — Group 1

D_2 Sporangia moderately to markedly papillate, nearly round (length/width ratio small, from 1.0:1.0 to 1.2:1.0) — E

E_1 Sporangia deciduous, markedly papillate, oogonia average 28 μm, good growth (1-5 mm/day) on cornmeal agar at 30°C. — *P. cactorum*

E_2 Sporangia non-deciduous, moderately to markedly papillate, oogonia average 35 μm, little or no growth (<1 mm/day) on cornmeal agar at 30°C. — *P. pseudotsugae*

B_2 Oogonia with predominantly (>50%) amphigynous antheridia produced in single strain culture on clarified V-8 agar. Species with these characteristics have not been reported from Northwest conifers.

B_3 Oogonia rarely produced in clarified V-8 agar in absence of opposite strain — F

F_1 Slow growing on cornmeal agar (2-4 mm/day at 20°C), isolated from *Chamaecyparis* species. — *P. lateralis*

F_2 Moderate to fast growing on cornmeal agar (4-9 mm/day at 20°C) — G

G_1 Mycelium with numerous small hyphal swellings. — *P. cinnamoni*

G_2 Mycelium without numerous hyphal swellings. — H

H_1 Colony appressed with dense rosettes of sharp, compact petals on clarified V-8 agar (Figure 2), and moderate growth (4-6 mm/day at 20°c) on cornmeal agar. — *P. drechsleri*

H_2 Colony aerial with slight or no pattern on clarified V-8 agar (Figure 2), and fast-growing (5-9 mm/day at 20°C) on cornmeal agar. Sporangia 37-55 x 23-30 μm; oogonia smooth-walled in paired culture. — *P. cryptogea*

H_3 Colony aerial, without pattern on clarified V-8 agar, and moderate growth (4-6 mm/day) on cornmeal agar. Sporangia large (58-73 x 38-45 μm); oogonia ornamented in paired culture. — *P. cambivora*

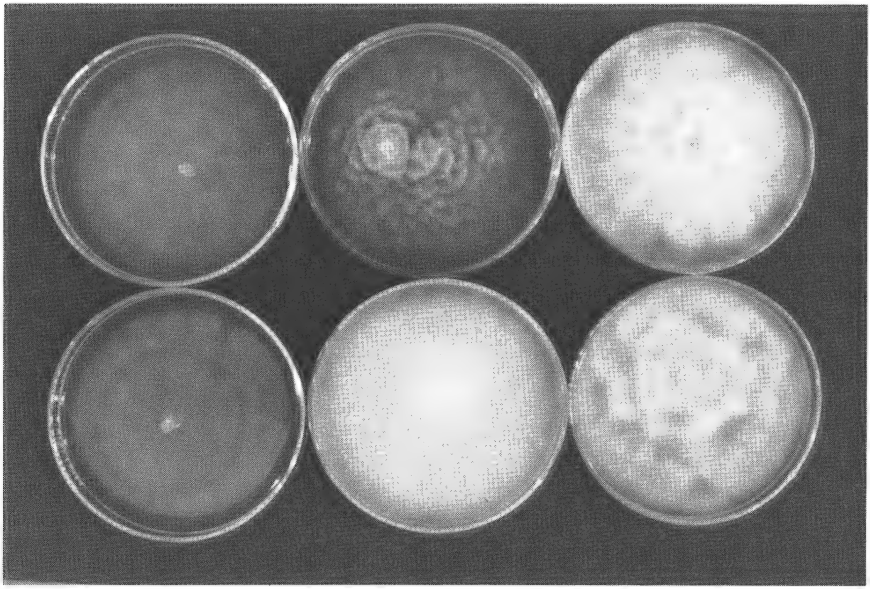

Figure 2. Growth characteristics of six *Phytophthora* species on clarified V-8 agar after 4 wks (top left to bottom right). *P. pseudotsugae, P. drechsleri, P. cinnamomi, P. lateralis, P. cryptogea* and *P. megasperma* Group 1. Notice aerial growth of *P. cinnamoni, P. cryptogea* and *P. megasperma.*

antibiotic, hymexazol, restricts growth of some *Pythium* species without affecting most *Phytophthora* (Hansen *et al.* 1979, Masago *et al.* 1977, Tsao and Guy 1977).

Pythium and *Phytophthora* isolates can be distinguished by hyphal and colony characteristics, but sporangial characteristics are more reliable, and are also important for distinguishing among *Phytophthora* species. Thus, growing isolates first in pea broth, then inducing sporangia in SEW, will simultaneously separate *Pythium* from *Phytophthora*, and allow determination of sporangial characteristics of the *Phytophthora* species. Isolates should also be grown on clarified V-8 agar to obtain information on oogonia (size and antheridial attachment) and other structures (chlamydospores or hyphal swellings), and on colony pattern. Growth rate on cornmeal agar (Difco) is also important for some species and should be determined prior to using the key. While all *Phytophthora* species known to be associated with Northwest conifers have been included, additional species may be isolated in the future. Therefore, as with any key, listed characteristics should be carefully considered to avoid mislabelling an unknown isolate.

Diagnostic Characteristics by Species

The following list includes characteristics that are especially helpful in identification of *Phytophthora* species recovered from Pacific Northwest conifers. Consult other sources (Newhook *et al.* 1978; Waterhouse 1963, 1970) for complete descriptions.

Phytophthora cactorum

A variable species worldwide, *P. cactorum* most closely resembles *P. pseudotsugae* in the Pacific Northwest. Sympodial production of ovoid to obpyriform, papillate, deciduous sporangia (size range 36-50 x 28-35 μm) on solid and liquid media is characteristic. *P. cactorum* usually produces abundant oogonia (size range 25-32 μm, generally smaller than *P. pseudotsugae*) with paragynous antheridia and mature oospores.

Chlamydospores are rarely formed. Unlike *P. pseudotsugae, P. cactorum* rots apple fruits within two weeks when a small agar plug containing the fungus is inserted into a hole made by a cork borer and covered with tape. *P. cactorum* causes root rot of Douglas-fir (*Pseudotsugae*

menziesii) and true fir (*Abies* sp.) in Oregon and Washington forest tree nurseries. It is also an important pathogen of certain orchard and ornamental crops in this region.

Phytophthora cambivora

This species is heterothallic, moderate-fast growing and patternless with aerial mycelium on clarified V-8 agar. *P. cambivora* generally grows more slowly than *P. cryptogea,* and produces larger sporangia (58-73 x 38-45 μm), and oogonia (39-51 μm). Oogonia are distinctly ornamented and antheridia commonly are two-celled. It lacks the numerous hyphal swellings and chlamydospores of *P. cinnamomi* on clarified V-8 agar.

P. cambivora is best known in the Northwest as a root and collar pathogen of fruit trees. This species was recently isolated from dead roots and girdling stem cankers on 2-5 year old Noble fir in a number of Christmas tree plantations in Oregon, but pathogenicity has not yet been confirmed (P. B. Hamm and G. A Chastagner, unpublished data).

Phytophthora cinnamomi

This species, like *P. lateralis,* readily produces chlamydospores (average 41 μm) in culture. *P. cinnamomi* grows much faster on cornmeal agar than *P. lateralis* (4-8 versus 1-2 mm/day respectively, at 20°) and has numerous hyphal swellings (Figure 2g). Sporangia (size range 27-114 x 20-71 μm) are persistent, non-papillate, ellipsoid to ovoid and form on unbranched sporangiophores. Oogonia, with amphigynous antheridia (size range 21-58 μm), form only in paired culture.

P. cinnamomi has been known to cause extensive damage to Douglas-fir only once in a Pacific Northwest forest tree nursery (Kanaskie pers. comm.). Damage has also been seen in rooted cuttings of Douglas-fir before and after transplanting in seed orchards and in Noble fir grown for Christmas trees. This species affects a wide number of ornamental plant species in this region, including *Taxus, Chamaecyparis, Pseudotsuga, Abies,* and other conifers (see Zentmyer 1980).

Phytophthora cryptogea

This species is fast growing, heterothallic, and produces a patternless, aerial colony on clarified V-8 agar (Figure 2). Hyphal swellings and chlamydospores are not produced. Sporangia are smaller than *P. cambivora* (range 37-55 x 23-30 μm) they are non-papillate, persistent, and ovoid. Oogonia are smooth walled and smaller (30-38 μm) than *P. cambivora,* having a single-celled amphigynous antheridium.

P. cryptogea has caused root rot of Douglas-fir in British Columbia, Washington and Oregon nurseries, true fir in Washington nurseries and in Oregon Christmas tree plantations, and sugar pine (*Pinus lambertiana*) in a Southern Oregon seed orchard.

Phytophthora drechsleri

P. drechsleri occasionally produces sporangia in solid media in isolation plates, a characteristic similar to *P. cactorum.* Chlamydospores form infrequently compared to *P. lateralis* or *P. cinnamomi.* The radiating, strongly rosette pattern of the colony formed on clarified V-8 agar is distinctive (Figure 2). Sporangia (size range 36-70 x 26-40 μm) are nonpapillate, persistent, and elongated, produced on sympodially branched sporangiophores. Oogonia (size range 36-53 μm) with amphigynous antheridia form only when colonies are paired with isolates of the opposite mating type.

P. drechsleri has been isolated from Douglas-fir in British Columbia, Oregon, and Washington nurseries, from forest soil in southeast Alaska and southwest Oregon, and from Noble fir Christmas trees in Oregon.

Phytophthora lateralis

Though placed here with heterothallic species to ease identification, *P. lateralis* is homothallic, forming oogonia only after 8-12 wks in Port-Orford-cedar foliage extract agar (Trione 1974). Growth rate at optimum temperature (2-3 mm/day at 20°) is the slowest of all *Phytophthora* species from conifers in this region. Sporangia on sympodially branched sporangiophores are persistent, non-papillate and mostly ovate or pyriform averaging 59 x 35 μm. Oogonia (size range 33-50 μm) have paragynous antheridia. Large numbers of chlamydospores (average size 40 μm) often form in clarified V-8 agar. Apple fruits are rotted very slowly or not at all.

Phytophthora lateralis reportedly attacks trees in the genus *Chamaecyparis* exclusively

(Torgeson *et al.* 1954). Port-Orford-cedar (*Chamaecyparis lawsoniana*), a tree native to southwest Oregon and northwest California, has been planted extensively as an ornamental throughout western Oregon, Washington, and British Columbia, and mortality from *P. lateralis* has been reported in each of these areas. The fungus is highly destructive in the forest.

Phytophthora megasperma Group 1

P. megasperma is a variable species worldwide with a number of distinct subgroups. Two subgroups, differing in morphology, growth characteristics, pathogenicity, host range, and response to metalaxyl (a very specific fungicide), have been recovered from Douglas-fir nursery stock in Oregon. Oogonia of isolates belonging to Group 1 average <44 μm in size, are not as pigmented on clarified V-8 agar as those from Group 2, and are generally produced in large numbers. Optimum growth occurs at 27°C, but isolates also grow well (1-2 mm/day) at 35°C. Isolates from Group 1 are inhibited (80% growth reduction) by metalaxyl (*in vitro*) at 1 μg/ml (Hansen and Hamm 1983, Hunger *et al.* 1982). Isolates of *P. megasperma* Group 1 are more aggressive in pathogenicity studies than *P. megasperma* Group 2 (Hamm and Hansen 1981, 1982a). Sporangia on unbranched sporangiophores (average size 53 x 35 μm) are persistent, non-papillate, and mostly ovoid. Oogonia with predominantly paragynous antheridia form in single-strain culture. Chlamydospores are lacking.

Phytophthora megasperma Group 1 has been found killing Douglas-fir roots in only one Oregon forest nursery.

Phytophthora megasperma Group 2

Oogonia average >46 μm in size, are usually distinctly pigmented light or yellow-brown and generally are not produced in large quantities on clarified V-8 agar. Optimum growth temperature is 22°C. The fungus will not grow at 35°C. Growth inhibition (*in vitro*) by metalaxyl at 1 μg/ml is 45% (Hansen and Hamm 1983, Hunger *et al.* 1982). Sporangial characteristics are similar to those of *P. megasperma* Group 1.

P. megasperma Group 2 has been found on Douglas-fir in Washington and Oregon nurseries, and on true fir and sugar pine only in Oregon nurseries. Group 2 isolates of *P. megasperma* are not as aggressive on Douglas-fir as isolates from Group 1 (Hamm and Hansen 1981, 1982a).

Phytophthora pseudotsugae

This species, closely resembling *P. cactorum*, differs by producing larger oogonia (average size >32 μm), oospores that often abort, persistent papillate sporangia (average size 39 x 32 μm) produced rarely in solid media and infrequently in liquid media, and has a lower optimum temperature for growth (20-25 versus 25-27°C for *P. cactorum*).

P. pseudotsugae does not produce pigment on casein hydrolysate-tyrosine medium, is sensitive to malachite green, and in contrast to *P. cactorum*, does not decay apple fruits (Hamm and Hansen 1983, Ho 1981). *Phytophthora pseudotsugae* rarely forms hyphal swellings, does not form chlamydospores, and nearly always has paragynous antheridia.

Phytophthora pseudotsugae has been found only in Oregon and Washington forest nurseries where it attacks Douglas-fir seedlings.

Acknowledgments

The authors would like to thank S. J. Cooley, S. Frankle, A. Kanaskie, J. T. Kliejunas, R. G. Linderman, R. Novak and O. K. Ribeiro for manuscript review, and N. L. Bobadilla for typing the manuscript.

This is publication number 2136 of the Forest Research Laboratory, Oregon State University, Corvallis, OR.

Literature Cited

Eckert, J. W., and P. H. Tsao. 1962. A selective antibiotic medium for the isolation of *Phytophthora* and *Pythium* from plant roots. Phytopathology 52:771-777.

Hamm, P. B., S. J. Cooley, and E. M. Hansen. 1984. Response of *Phytophthora* spp. to metalaxyl in forest tree nurseries in the Pacific Northwest. Plant Dis. 68:671-673.

Hamm, P. B., and E. M. Hansen. 1981. Host specificity of *Phytophthora megasperma* from Douglas-fir, soybean, and alfalfa. Phytopathology 71:65-68.

_____. 1982a. Pathogenicity of *Phytophthora* spp. to Northwest conifers. Eur. J. For. Pathol. 12:167-174.

_____. 1982b. Single-spore isolate variation: the effect on varietal designation in *Phytophthora megasperma*. Can. J. Bot. 12:2931-2938.

_____. 1983. *Phytophthora pseudotsugae,* a new species causing root rot of Douglas-fir. Can. J. Bot. 61:2626-2631.

_____. 1984. Improved method for isolating *Phytophthora lateralis* from soil. Plant Dis. 68:517-519.

Hamm, P. B., E. M. Hansen, and J. R. Sutherland. 1985. *Phytophthora cryptogea* and *P. drechsleri* associated with root rotted Douglas-fir seedlings in British Columbia. Plant Dis. 69:361.

Hansen, E. M., and P. B. Hamm. 1983. Morphological differentiation of host specialized groups of *Phytophthora megasperma.* Phytopathology 73:129-134.

Hansen, E. M., P. B. Hamm, A. J. Julis, and L. F. Roth. 1979. Isolation, incidence and management of *Phytophthora* in forest tree nurseries in the Pacific Northwest. Plant Dis. Rep. 63:607-611.

Hansen, E. M., L. F. Roth, P. B. Hamm, and A. J. Julis. 1980. Survival, spread, and pathogenicity of *Phytophthora* spp. on Douglas-fir trees planted on forest sites. Phytopathology 70:422-425.

Ho, H. H. 1981. Synoptic keys to the species of *Phytophthora.* Mycologia 73:705-714.

Hunger, R. M., P. B. Hamm, C. E. Horner, and E. M. Hansen. 1982. Tolerance of *Phytophthora megasperma* isolates to metalaxyl. Plant Dis. 645-649.

Kliejunas, J. T., and D. H. Adams. 1981. Phytophthora root rot of Port-Orford-cedar in California. Plant Disease 65:446-447.

Linderman, R. G., and F. Zeitoun. 1977. *Phytophthora cinnamomi* causing root rot and wilt of nursery-grown native western azalea and salal. Plant Dis. Rep. 61:1045-1048.

Masago, H., M. Yoshikawa, M. Fukada, and N. Nakanishi. 1977. Selective inhibition of *Pythium* spp. on medium for direct isolation of *Phytophthora* spp. from soils and plants. Phytopathology 67:425-428.

McIntosh, D. L. 1966. The occurrence of *Phytophthora* spp. in irrigation systems in British Columbia. Can. J. Bot. 44:1591-1596.

Received 21 July 1986
Accepted for publication 3 November 1986

Newhook, F. J., G. M. Waterhouse, and D. J. Stamps. 1978. Tabular key to the species of *Phytophthora* de Bary. Commonw. Mycol. Inst. Mycol. Pap. No. 143.

Ostrofsky, W. D., R. G. Pratt, and L. F. Roth. 1977. Detection of *Phytophthora lateralis* in soil organic matter and factors that affect its survival. Phytopathology 67:79-84.

Pratt, R. G., and J. E. Mitchell. 1973. A new species of *Pythium* from Wisconsin and Florida isolated from carrots. Can. J. Bot. 51:333-339.

Pratt, R. G., L. F. Roth, E. M. Hansen, and W. D. Ostrofsky. 1976. Identity and pathogenicity of species of *Phytophthora* causing root rot of Douglas-fir in the Pacific Northwest. Phytopathology 66:710-714.

Roth, L. F., E. J. Trione, and W. H. Ruhmann. 1957. *Phytophthora* induced root rot of native Port-Orford-cedar. J. Forestry 55:294-298.

Torgeson, D. C., R. A. Young, and J. A. Milbrath. 1954. *Phytophthora* root rot diseases of Lawson cypress and other ornamentals. Oreg. Agric. Exp. Sta., Sta. Bull. 537.

Trione, E. J. 1974. Sporulation and germination of *Phytophthora lateralis.* Phytopathology 64:1531-1533.

Tsao, P. H., and S. O. Guy. 1977. Inhibition of *Mortierella* and *Pythium* in a Phytophthora-isolation medium containing hymexazol. Phytopathology 67:796-801.

Tsao, P. H., and G. Ocana. 1969. Selective isolation of species of *Phytophthora* from natural soils on an improved antibiotic medium. Nature 223:636-638.

Waterhouse, G. M. 1963. Key to the species of *Phytophthora* de Bary. Commonw. Mycol. Inst. Mycol. Pap. No. 92.

_____. 1970. The genus *Phytophthora* de Bary. Commonw. Mycol. Inst. Mycol. Pap. No. 122.

Waterhouse, G. M., and E. M. Blackwell. 1954. Key to the species of *Phytophthora* recorded in the British Islands. Commonw. Mycol. Inst. Mycol. Pap. No. 57.

Zentmyer, G. A. 1980. *Phytophthora cinnamomi* and the diseases it causes. Am. Phytopathol. Soc., Monogr. 10.

Zobel, D. B., L. F. Roth, and G. M. Hawk. 1985. Ecology, Pathology, and Management of Port-Orford-cedar (*Chamaecyparis lawsoniana*). Gen. Tech. Rep. PNW-184, Pacific Northwest Range and Experiment Station, USDA-Forest Service, Portland, Oregon.

Edward K. Johnson, Department of Zoology
Washington State University, Pullman, WA 99164-4220

Stability of Venoms from the Northern Pacific Rattlesnake (*Crotalus viridis oreganus*)

Abstract

Stability of proteins in venom samples extracted from twelve northern Pacific rattlesnakes (*Crotalus viridis oreganus*) over an eight month period (April-November, 1984) was demonstrated by SDS-polyacrylamide electrophoresis. The electrophoretic pattern of the venoms varied considerably between individual *C. v. oreganus*, but for the same individual remained identical from the time the rattlesnakes emerged from hibernation through their active, summer period. The electrophoretic variation of individual venoms did not appear to be a result of differences in geographic location or sex. Electrophoresis of the venoms revealed 8-14 protein components that ranged in molecular weight from approximately 6,000 to 66,000. The stability of the venoms suggests that the secretory epithelium of the venom glands maintain a consistent composition of proteins in the venoms. Thus, the effects of hibernation on venom composition are apparently negligible. Consequently, as *C. v. oreganus* emerge from hibernation they most likely maintain undiminished feeding and defensive capabilities.

Introduction

The northern Pacific rattlesnake (*Crotalus viridis oreganus*) is a subspecies of the western rattlesnake distributed in the temperate regions of the Pacific northwest, including northern California, Oregon, Washington, and parts of Idaho and British Columbia (Nussbaum *et al.* 1983). The *C. v. oreganus* from southeastern Washington are often subjected to extreme variations in climate due to seasonal changes. Environmental conditions range from hot, dry periods with temperatures exceeding 38°C during summer months (June-August) to prolonged periods of subfreezing temperatures in the winter (December-January). The rattlesnakes inhabiting this region survive the harsh winter conditions by hibernating for extended periods below the frost line in protected dens located throughout the area.

C. v. oreganus resume hunting soon after emergence from hibernation and continue throughout their active summer period. However, the effects that hibernation and seasonal changes have on the composition of *C. v. oreganus* venoms are not known. If the composition of venom changes during winter months, as in some snake species (Gubensek *et al.* 1974), then resumption of predatory and defensive behavior in the spring could be impaired.

In other species of venomous snakes, different species show different responses to seasonal change. Gubensek *et al.* (1974) have shown a difference in the electrophoretic migration of proteins in European long-nosed viper (*Vipera ammodytes*) venoms extracted during the winter months. Sket *et al.* (1973) also isolated two toxic proteins in the venoms from *V. ammodytes* that were absent in winter venom extractions. However, no change in venom composition occurred in jumping viper (*Bothrops nummifera*) venoms or in venoms from the African puff adder (*Bitis arietans*) regardless of the time of year the venoms were extracted (Jimmenz-Porras 1964, Willemse 1979). The purpose of the present investigation was to study the electrophoretic migration of venom proteins from newly captured *C. v. oreganus* collected early in the spring as they emerged from hibernation and compare the pattern to venoms extracted from the same individuals seven months later in the fall at the time of their normal return to hibernation to determine if any change occurs in the composition of their venoms.

Study Area and Methods

Two den sites located in Whitman and Lincoln counties of southeastern Washington State were checked regularly and northern Pacific rattlesnakes (*C. v. oreganus*) of both sexes collected early in April, 1984 as they emerged from hibernation. The rattlesnakes were sexed, measured, and housed in glass aquaria in an environmentally controlled room (25° + C; 12 hr. light/dark). The sizes of the *C. v. oreganus* used were: less than 50 cm (n = 2), 50-80 cm (n = 7), and greater than 80 cm (n = 3). The rattlesnakes were fed white mice of appropriate size approximately once a month throughout the investigation.

The *C. v. oreganus* were subjected to venom extraction within 24 hours of capture and then again seven months later in November, 1984. Venom samples from a total of 12 *C. v. oreganus* were individually collected into separate 1.5 ml plastic vials. The venoms were extracted by allowing each rattlesnake to bite naturally (no pressure applied to the venom glands) through a parafilm membrane stretched tightly over the opening of a glass funnel that emptied into the vials. The venoms were immediately frozen and then lyophilized at −50°C for 24 hours. The vials containing lyophilized venoms were stored over dessicant at −4°C in glass containers.

Electrophoresis

SDS-polyacrylamide electrophoresis (1.5 mm slab gel) was performed following Laemmli (1970) using a 4% stacking and 9% separating gel. The lyophilized venoms were reconstituted in sample buffer (pH 6.8) to a concentration of 2 mg/ml. Venoms extracted from the *C. v. oreganus* in April, 1984, and then again in November, 1984, were loaded into consecutive wells at a concentration of 0.08 mg venom per well. The electrophoresis (continuous current) was run at 5 mA/gel for 90 minutes followed by 30 mA/gel for 3 hours.

Upon completion of the electrophoresis, the gels were immediately stained in 0.001% Commassie Brilliant Blue (Sigma Chemical Co., Inc.) for 2-4 hours and destained using a 7% acetic acid, 35% methanol, and 58% distilled water solution. SDS-Dalton Mark VII-L markers (Sigma, Inc.) were used for approximate molecular weight determinations.

Results

The results of SDS-polyacrylamide electrophoresis of *C. v. oreganus* venoms extracted from three of the twelve individuals during the spring and fall, 1984, are shown in Figure 1. All twelve *C. v. oreganus* showed considerable individual differences in the protein components in their venoms, however, the composition of venom from the same snake did not change from April, 1984 through November, 1984.

SDS-polyacrylamide electrophoresis of crude venoms reduced with 2-mercaptoethanol revealed 8-14 protein components that ranged in molecular weight from approximately 6,000 to 66,000. The venoms contained two protein bands with molecular weights of approximately 30,000 and 60,0000 and two low molecular components of approximately 6,000 and 10,000 that appeared as dark staining bands in the gels and seemed to be present in all rattlesnake venoms used in the investigation. The remaining protein components in the venoms were not common to all rattlesnakes. The variation in electrophoretic pattern of protein components between individuals did not appear to correlate with the geographic location or the sex of the rattlesnakes.

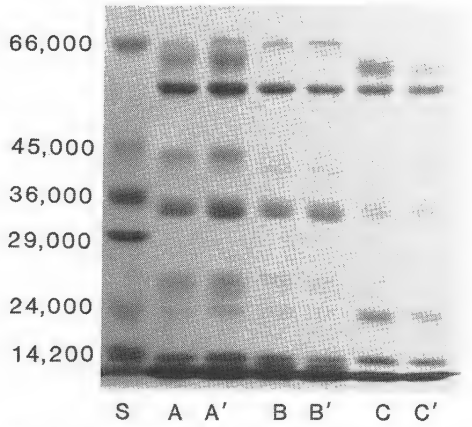

Figure 1. 9.0% SDS-polyacrylamide electrophoresis of *C. v. oreganus* venoms. Column S, molecular weight markers. Columns A, B, and C, venoms from three *C. v. oreganus* extracted during April, 1984. Columns A', B', and C', corresponding venoms from the same three rattlesnakes extracted seven months later.

Discussion

Numerous studies on snake venoms have demonstrated ontogenetic changes in the composition of venom proteins (Minton 1967, Fiero *et al.* 1972, Meirer 1986, Bonilla *et al.* 1973, Mackessy 1985). Geographic differences in the electrophoretic migration of venom proteins have also been shown in *Crotalus atrox* and *Bothrops asper* (Minton and Weinstein 1986, Aragon-Ortiz and Gubensek 1979). Furthermore, Gubensek *et al.* (1974) showed a seasonal variation in venoms from *V. ammodytes* even though the snakes were maintained in a controlled environment. The composition of venoms from other snake species, however, remained stable throughout the year (Jimenz-Porras 1964, Willemse 1979).

The venoms from captive *C. v. oreganus* maintained in a controlled environment over several years did not show any seasonal variation in the composition of proteins (unpublished results). SDS-polyacrylamide electrophoresis performed on the venoms from newly captured *C. v. oreganus* used in this experiment also revealed a consistency in venom proteins from the time the rattlesnakes emerged from hibernation (April) through their active summer period (May-October). The electrophoretic migration of venom proteins was observed for only one summer period to minimize the possibility of ontogenetic changes in composition.

The *C. v. oreganus* used in this experiment were maintained in a controlled environment that did not exactly duplicate natural environmental conditions. The rattlesnakes, however, were collected at a time when they were normally becoming active after a long period of hibernation. If hibernation had affected venom composition, then the electrophoretic migration of venoms collected as the snakes emerged in the spring should have been different from samples extracted after the snakes had been active throughout the summer, even though they were housed in a controlled environment. Since the venoms did not change, it seems likely that the effects of hibernation, if any, are very slight.

The stability of *C. v. oreganus* venoms implies that the secretory epithelium of the venom glands maintains a consistent composition and thus maintains the feeding and defensive capabilities of the snakes as they emerge from hibernation in the spring. Willemse (1979) proposed that the length of time the venom remains in the lumen of the venom glands could ultimately cause changes in the electrophoretic migration of proteins. Crotalid and viperid snake venoms normally contain numerous proteolytic enzymes (Bjarnason and Tu 1978, Kocholaty *et al.* 1971, Kurecki *et al.* 1978) that could produce peptide artifacts in the venoms through auto-cleavage of the proteins. The *C. v. oreganus* used in this investigation were feeding regularly and the venoms were not stored in the glands for identical periods between extractions. The electrophoretic pattern of the venoms from individual rattlesnakes, however, was identical in both spring and fall venom extractions. The length of time the venom remains in the glands of *C. v. oreganus* thus does not appear to be a significant factor determining the electrophoretic migration of venom proteins.

Intrasubspecific differences in the composition of individual snake venoms have been well documented (Meirer 1986). The *C. v. oreganus* from southeastern Washington also showed considerable individual variation in the electrophoretic migration of proteins in their venoms (Figure 1). The high degree of variation in protein components required that the venoms from individual *C. v. oreganus* be examined to prevent the possibility of intrasubspecific differences in pooled samples being interpreted as a change in composition.

It was not possible to sample venom from *C. v. oreganus* during actual hibernation with the experimental procedure used in this investigation. An undetected change in composition could have occurred but is rapidly stabilized once the rattlesnakes start to emerge in the spring. However, the present study suggests that *C. v. oreganus* in southeastern Washington demonstrate a stable electrophoretic migration of proteins in their venoms as they emerge from hibernation and throughout their active, summer period (April-October).

Acknowledgments

I would like to thank Kenneth V. Kardong for the use of laboratory facilities, support, and comments on the manuscripts. Special thanks are given to Darwin K. Vest for his advice and knowledge of snake venoms and Brian Miller for assistance in collecting the rattlesnakes. I would also like to thank John H. Larsen, Howard L. Hosick, Raymond Reeves, Paul C. Schroeder, and associated lab personnel for the use of laboratory equipment. This work was supported by Grant BNS 7817465 from the National Science Foundation, Psychobiology Program to K. V. Kardong.

Literature Cited

Aragon-Oritz, F., and F. Gubensek. 1979. *Bothrops asper* venom from the Atlantic and Pacific zones of Costa Rica. Toxicon 19:797-805.

Bjarnason, J. B., and A. T. Tu. 1978. Hemorrhagic toxins from the western diamondback rattlesnake (*Crotalus atrox*): Isolation and characterization of five toxins and the role of zinc in hemorrhagic toxin e. Biochemistry 17:3395-3403.

Bonilla, C. A., M. R. Faith, and S. A. Minton. 1973. l-aminoacid oxidase, phosphodiesterase, total protein, and other properties of juvenile timber rattlesnake (*Crotalus horridus*) venom at different stages of growth. Toxicon 11:301-303.

Fiero, M. K., M. W. Seifert, T. J. Weaver, and C. A. Bonilla. 1972. Comparative study of juvenile and adult prairie rattlesnake (*Crotalus v. viridis*) venoms. Toxicon 10:81-82.

Gubensek, F., D. Sket, V. Turk, and D. Lebez. 1974. Fractionation of *Vipera ammodytes* venom and seasonal variation of its composition. Toxicon 12:167-171.

Jimenez-Porras, J. M. 1964. Intraspecific variations in composition of venoms of the jumping viper (*Bothrops nummifera*). Toxicon 2:187-195.

Kocholaty, W. F., E. B. Ledford, J. G. Daly, and T. A. Billings. 1971. Toxicity and some enzymatic properties and activities in the venoms of Crotalidae, Elapidae, and Viperidae. Toxicon 9:131-138.

Kurecki, T., M. Laskowski, Sr., and L. F. Kress. 1978. Purification and some properties of two proteinases from *Crotalus adamenteus* venoms that inactivate alpha-proteinase inhibitor. J. Biol. Chem. 253: 8340-8345.

Received 25 August 1986
Accepted for publication 10 October 1986

Laemmli, U. K. 1970. Cleavage of structural proteins during assembly of the head of the bacteriophage T4. Nature 227:680-685.

Mackessy, S. P. 1985. Fractionation of red diamond rattlesnake (*Crotalus ruber ruber*) venom: protease, phosphodiesterase, L-amino acid oxidase activities and effects of metal ions and inhibitors on protease activity. Toxicon 23:337-340.

Meirer, J. 1986. Individual and age-dependent variations in the venom of the fer-de-lance (*Bothrops atrox*). Toxicon 24:41-46.

Minton, S. A. 1967. Observations on toxicity and antigenic make-up of venoms from juvenile snakes. *In* Animal Toxins (F. E. Russel and P. R. Saunders, eds.) Oxford/Pergamon Press. Pp. 211-222.

S. A. Weinstein. 1986. Geographic and ontogenetic variation in venoms of the western diamondback rattlesnake (*Crotalus atrox*). Toxicon 24:71-80.

Nussbaum, R. A., E. D. Brodie, and R. M. Storm. 1983. Amphibians and reptiles of the Pacific Northwest. University Press of Idaho, Moscow.

Sket, D., F. Gubensek, S. Adamic, and D. Lebez. 1973. Action of a partially purified basic protein fraction from *Vipera ammodytes*. Toxicon 11:47-53.

Willemse, G., J. Hattingh, and R. Karlsson. 1979. Changes in composition and protein concentration of puff adder (*Bitis arietans*) venoms due to frequent milking. Toxicon 17:37-42.

Frank B. Isaacs and **Robert G. Anthony,** Oregon Cooperative Wildlife Research Unit
Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331-3803

Abundance, Foraging, and Roosting of Bald Eagles Wintering in the Harney Basin, Oregon

Abstract

Bald eagles (*Haliaeetus leucocephalus*) were observed in the Harney Basin, Oregon, during the winters of 1982-83 and 1984. The number of bald eagles peaked at ~170 during 28 February-6 March 1983 and ~180 during 19-25 March 1984. Both peaks coincided with large numbers of migrating waterfowl in the basin. Eagles foraged primarily on waterfowl from November to December, on mammal carrion from December to February, and again on waterfowl from February to April. Fifteen communal roosts were located; eight were in ponderosa pine (*Pinus ponderosa*) stands in the forested foothills of the Blue Mountains, and seven were in deciduous trees on the basin floor. Coniferous roost trees were the largest, dominant or codominant trees in roost stands. Most (98%) roost trees were larger than the USDA Forest Service minimum old-growth specifications for the ponderosa pine forest type. Management of bald eagle habitat in the Harney Basin should include maintenance of old-age trees, planting of deciduous trees close to feeding sites, avoidance of activity that drastically changes normal seasonal flooding patterns, and encouragement of ranchers to leave cow carcasses available for eagles.

Introduction

Bald eagles congregate where food is abundant during the non-breeding season and often use communal night roosts near these foraging areas. Recent studies have described abundance, food habits, and roosting habitat of bald eagles during autumn (McClelland *et al.* 1982, Anthony *et al.* 1982), migration (Young 1983), and winter (Keister *et al.* 1987, Keister and Anthony 1983, Anthony *et al.* 1982, Reynolds *et al.* 1985) in the Pacific Northwest.

Numbers of bald eagles observed during winter in the Harney Basin, Oregon, have increased steadily since 1940 (Malheur National Wildlife Refuge 1939-1982, this study). The maximum monthly count for each winter averaged 2 ($n = 3$, SE = 0.6) from 1941 to 1950, 11 ($n = 8$, SE = 2.2) from 1951 to 1960, 18 ($n = 10$, SE = 2.5) from 1961 to 1970, 28 ($n = 10$, SE = 7.9) from 1971 to 1980, and 118 ($n = 4$, SE = 35.3) from 1981 to 1984. In 1978, a bald eagle communal roost was found 7.4 km north of the Harney Basin in the foothills of the Blue Mountains (Thompson and Littlefield 1983). Because of the threatened status of the species (U.S. Dept. Interior 1978), concerns about the possible effects of oil and gas leasing and timber management practices on the roost were raised. This study was initiated in November 1982 to describe abundance, foraging behavior, and roosting habitat of bald eagles in the Harney Basin of southeastern Oregon.

Study Area

The study area included the Harney Basin and adjacent foothills of the Blue, Stinkingwater, and Steens Mountains, and a 40-km section of the Malheur River in the northeastern corner of Harney Co., Oregon (Figure 1). The Harney Basin is located in southeastern Oregon and includes both Harney and Malheur Lakes. Malheur Lake is the largest freshwater marsh in the western United States and is one of the most important resting and feeding areas for northward-migrating waterfowl of the Pacific Flyway (Paullin and Littlefield 1977). Elevations ranged from 1244 m at Harney Lake to 2967 m on Steens Mountain. The climate is semi-arid with low annual precipitation ($\bar{x} = 30.05$ cm), low humidity, and a wide range between daily maximum and minimum temperatures (U.S. Dept. Commerce 1981). Major vegetation zones vary by elevation and are steppe, shrub-steppe, desert shrub, juniper (*Juniperus occidentalis*), and ponderosa pine (Franklin and Dyrness 1973). The basin floor is relatively flat and is a mosaic of seasonally wet or flooded meadows, periodically dry lake beds, steppe and shrub-steppe plant communities, and scattered individual and small groups of deciduous trees.

Methods

We conducted feeding ground counts weekly from November 1982 to mid-March 1983, biweekly between January and mid-March 1984,

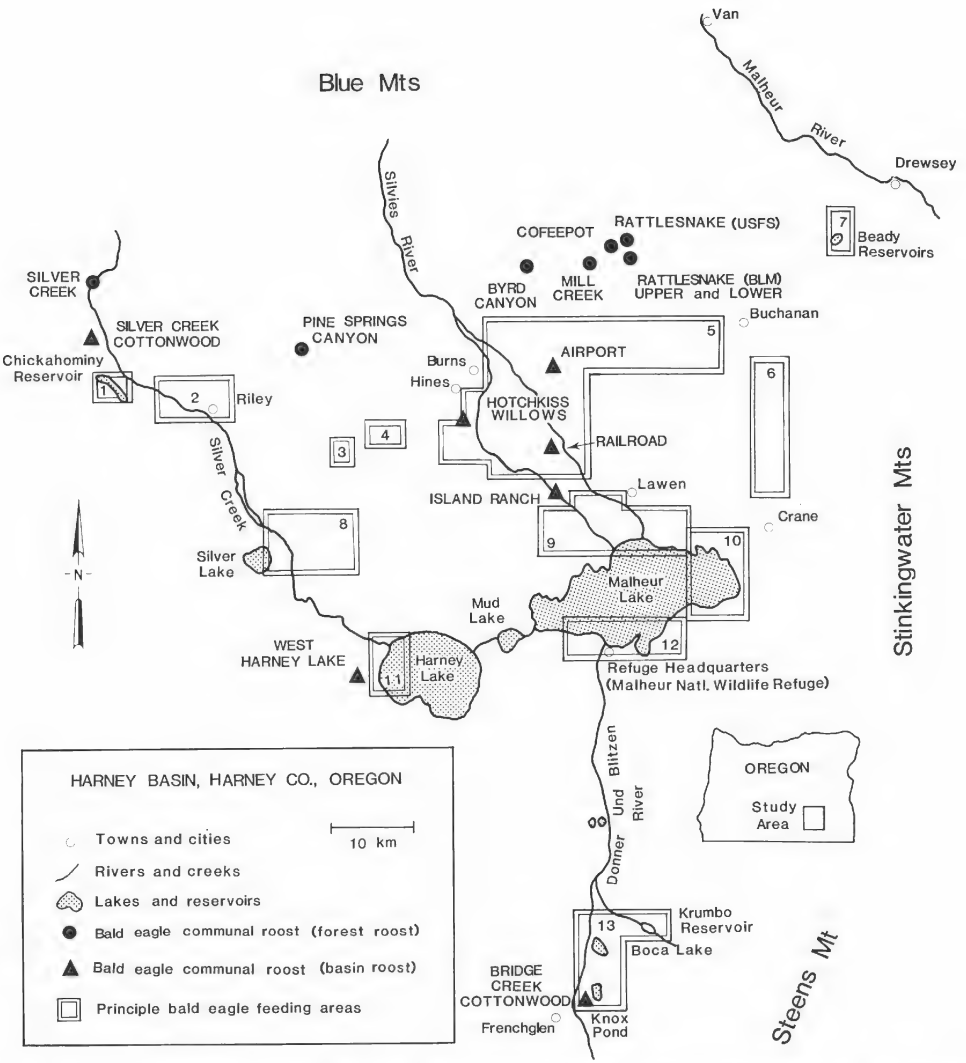

Figure 1. Study area with principal feeding areas and roosts used by wintering bald eagles during 1982-83 and 1984 in the Harney Basin, Oregon.

and weekly from mid-March to mid-April 1984. These counts were used to determine the number of bald eagles feeding in the basin and to locate their principal feeding areas. The counts were made by one person driving all-weather roads and attempting to locate every bald eagle that was visible with a 45X spotting scope. To accomplish this, we drove at slow speeds (16-64 km/hr), stopped often (0.4-3.2 km), and hiked to elevated viewpoints to search for eagles. Age class (adult = all white head and tail, subadult = any degree of brown in head or tail feathers, or unknown), location, and time were recorded for each eagle observed.

If a consistent pattern of long-distance flights by bald eagles to or from a particular area was observed, that area was searched by ground or air for a communal roost site. Three flights with

fixed-wing aircraft and three by helicopter were used to search for and verify communal roosts by observing eagles in roosts at dusk. Roost counts were conducted weekly unless bad weather interfered. Counts of eagles leaving roosts in conifer stands were made at dawn from vantage points between roosts and principal feeding areas. Counts of eagles roosting in deciduous trees on the basin floor were made at dawn and/or dusk from a vehicle on the nearest public road. Age class, flight direction and altitude, and time were recorded for each bald eagle flying from or to roosts.

Characteristics (species, diameter at breast height [dbh], height, and structure classification [Figure 2]) of trees >30.5 cm dbh in communal roosts were measured during July 1983 and 1984.

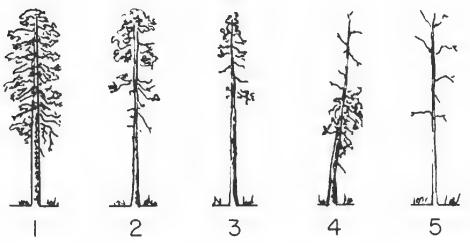

Figure 2. Structures used to classify trees within bald eagle communal roosts in conifer stands in the Harney Basin, 1983-84 (as adapted from Keen [1943]).

The 30.5 cm dbh limit was used because smaller trees were unavailable for roosting due to their small size and flimsy branches. A tree was considered a roost tree if there were one or more castings below the tree. Stand characteristics were described using the point-centered-quarter method (Mueller-Dombois and Ellenburg 1974, 110-120) at the Coffeepot Creek and Rattlesnake Creek (FS) roosts. At Pine Springs Canyon and Rattlesnake Creek (BLM), density of stands was determined by complete enumeration because of their small size. Roost tree characteristics were described by complete enumeration at Pine Springs Canyon and at Rattlesnake Creek roosts and by a systematic sample (the closest roost tree to each of 20 point-centered-quarter plots was measured) at Coffeepot Creek. Castings below all roost trees were counted and categorized by primary composition (i.e. fur or feathers).

Results and Discussion

Abundance and Foraging Habits—The greater of total weekly roost counts or feeding ground counts was used as an estimate of the number of eagles in the Basin (Table 1). We used the greater count because roost counts were seldom complete due to unknown roosts or bad weather. Variations in weather, observer, day of count, and time of day (for feeding-ground counts) affected counts to a different extent each week.

TABLE 1. Total weekly feeding ground and roost counts and the resultant population estimate of bald eagles in the Harney Basin, Oregon.

Week	Feeding Ground Count	Roost Count	Population Estimate
1982-1983			
1-6 Nov	1	0	1
7-14 Nov	7	0	7
15-21 Nov	9	0	9
22-28 Nov	18	1	18
29 Nov-5 Dec	15	0	15
6-12 Dec	13	1	13
13-19 Dec	16	1	16
20-26 Dec	20	7	20
27 Dec-2 Jan	15	5	15
3-9 Jan	22	16	22
10-16 Jan	28	18	28
17-23 Jan	25	15	25
24-30 Jan	34	33	34
31 Jan-6 Feb	43	16	43
7-13 Feb	42	19	42
14-20 Feb	48	50	50
21-27 Feb	62	91	91
28 Feb-6 Mar	173	128	173
7-13 Mar	110	128	128
14-20 Mar	120	131	131
21-27 Mar	-	69	69
28 Mar-3 Apr	-	81	81
4-10 Apr	-	21	21
11-17 Apr	-	16	16
1984			
16-22 Jan	20	15	20
23-29 Jan	-	16	16
30 Jan-5 Feb	17	24	24
6-12 Feb	-	19	19
13-19 Feb	38	27	38
20-26 Feb	-	55	55
27 Feb-4 Mar	52	56	56
5-11 Mar	-	49	49
12-18 Mar	111	70	111
19-25 Mar	182	175	182
26 Mar-1 Apr	103	121	121
2-8 Apr	62	57	62
9-15 Apr	21	29	29

– = No Data

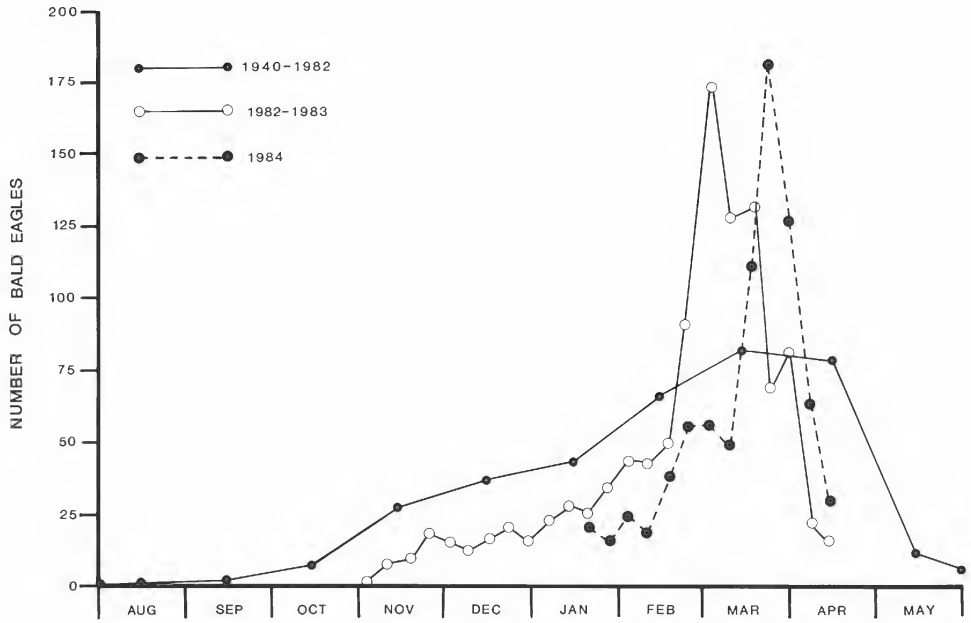

Figure 3. Numbers of bald eagles observed in the Harney Basin, Oregon. (January 1940-October 1982 data are maximum monthly counts and were compiled from files of Malheur National Wildlife Refuge, U.S. Fish and Wildlife Service; Southeast Regional Office, Oregon Dept. of Fish and Wildlife; and Burns and Snow Mountain Ranger Districts, U.S. Forest Service; 1982-83 and 1984 data are the maximum of weekly ground or roost counts.)

Bald eagles were in the Harney Basin from August through May. The maximum numbers of eagles observed was 170 during 28 February-6 March 1983 and 182 during 19-25 March 1984 (Table 1, Figure 3). Some of the increase over previous years was due to increased effort by observers. In addition, more eagles may have used the Harney Basin because of habitat changes that reduced food supplies in other parts of the Pacific Northwest (Thompson and Littlefield 1983). Numbers of bald eagles at Glacier National Park and in the Klamath Basin of Oregon and California also appear to have increased recently with an increase in available food (McClelland *et al.* 1982, Keister *et al.* 1987).

Carrion and waterfowl were the most obvious food items utilized by bald eagles during this study. Bald eagles were observed on or near large mammal carcasses on 24 occasions. Twenty-one (88%) of those observations were at cow carcasses and three were at deer carcasses. Utilization of cow carcasses was observed most often during the late December to mid-February period when 17 (81%) observations were made and when only small numbers of migrant waterfowl (Figure 4) were present in the basin. Of 1,940 castings examined, 1,656 (86%) were composed primarily of feathers, and 209 (11%) were composed primarily of fur.

The distribution of bald eagles in the Harney Basin was apparently food related. Weather patterns caused habitat changes that affected food quantity and distribution. Normal weather in the basin caused gradual freezing (October-December) and thawing (February-April) of water bodies and heavy runoff from snowmelt. From October to December, numbers of bald eagles usually were associated with concentrations of waterfowl at open water (Figure 1, principal feeding areas 7, 10, 11, 12, 13). From December to February, water bodies were frozen and eagle numbers increased slightly. During this time,

they were observed foraging mainly on mammal carrion in sagebrush and meadow areas (Figure 1, principal feeding areas 1, 3, 5, 13). Relatively few waterfowl were in the basin at this time. Between February and April, open water increased as lakes and ponds thawed and meadows flooded. This provided habitat for an enormous influx of northward-migrating waterfowl (Figure 4) and coincided with a dramatic increase in bald eagles (Figure 3) in the Basin (Figure 1, principal feeding areas 2, 4-5, 8-13). Other prey became available during this time. Carp (*Cyprinus carpio*) and other fish which had died in shallow ponds over winter were no longer covered by ice; ground squirrels (*Spermophilus* spp.) emerged; and various species of rodents were drowned or forced to the surface as fields flooded.

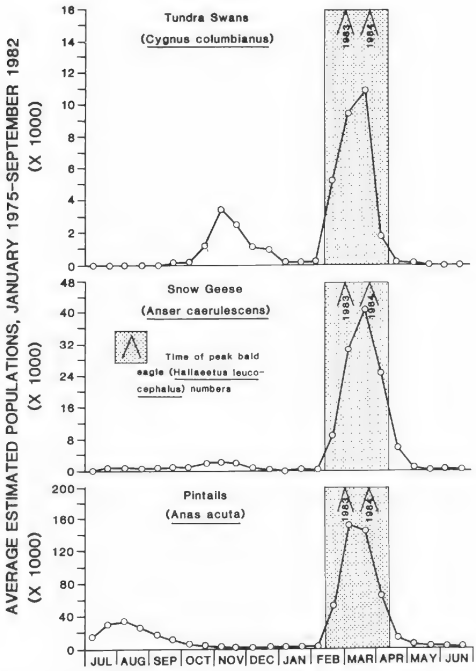

Figure 4. Population estimates of the most abundant waterfowl species during 1975-1982 in the Harney Basin, Oregon (compiled from files of Malheur National Wildlife Refuge, U.S. Fish and Wildlife Service).

Observations suggested that the Harney Basin was utilized by winter resident and spring migrant bald eagles. Peak counts of eagles at Glacier National Park occurred in November and declined through December (McClelland *et al.* 1982), which coincided with an influx of eagles in the Harney Basin (this study) and the Klamath Basin (Keister *et al.* 1987). Our counts and observations of one color-marked bald eagle (S. Thompson, pers. comm.) plus one equipped with a radiotransmitter (Young 1983) suggested that some eagles wintered in the Harney Basin, while most used the basin during spring migration. Highest counts of bald eagles at wintering areas in northeastern Nevada (Beck 1980), southern California (Walter and Garrett 1981), and the Klamath Basin occurred in late January and early February (Keister *et al.* 1987). These numbers declined as numbers of eagles in the Harney Basin increased in late February and March (Figure 3). The Harney Basin apparently is an important stopping place for many northward-migrating bald eagles.

The number of individual bald eagles that used the Harney Basin probably was higher than our maximum counts. Young (1983) followed bald eagles marked with radio transmitters in Glacier National Park and found a mean residency in the park of 11 days following capture. He also observed movements of radio-equipped bald eagles at American Falls Reservoir, Idaho, and found that as many as five times the maximum daily count of bald eagles may have used that area for periods ranging from one day to all winter. If this pattern of use exists in the Harney Basin, as many as 1,000 individual bald eagles may use the area annually.

Roosting Habits—Bald eagles were observed at 15 communal roosts in the Harney Basin. Eight were located in the foothills of the Blue Mountains in conifer stands dominated by ponderosa pine which were the closest such stands to principal feeding areas. Seven roosts were single or small groups of deciduous trees (cottonwood [*Populus deltoides*]), willow [*Salix* spp.], or European white poplar [*Populus alba*] located on the basin floor near the principal feeding areas (Figure 1). This combination of forest and basin roosts is similar to roosting habitat observed in Utah (Edwards 1969, Platt 1976, Young 1983) and Idaho (Reynolds *et al.* 1985), but different from the Klamath Basin (Keister and Anthony 1983) where few deciduous trees were available near the feeding areas.

Bald eagles are opportunistic foragers and in winter often roost communally near a major

TABLE 2. Characteristics of forest stands and roost trees at five communal roosts used by bald eagles in the Harney Basin, Oregon. All trees measured were >30.5 cm diameter at breast height (dbh).

Roost Name	Roost Size (ha)	Density (Trees/ha)	dbh (cm)[a] Stand Trees	dbh (cm)[a] Roost Trees	Height (m)[a] Stand Trees	Height (m)[a] Roost Trees	Structure Classification[ab] Stand Trees	Structure Classification[ab] Roost Trees	% Spike-topped and Snag Trees Stand	% Spike-topped and Snag Trees Roost
Pine Springs Canyon	4.6	53.7	20 57.8 15.6	43 69.6 9.5	20 25.5 5.9	43 31.2 3.8	20 1.53 0.47	43 2.00 0.82	0	5
Coffeepot Creek	28.3	82.5	88 53.1 24.2	20 87.5 16.1	88 21.2 8.7	20 36.8 7.7	88 1.47 1.02	45 2.67 1.46	7	28
Rattlesnake Creek-FS	19.8	71.8	100 49.6 19.7	100 74.1 11.5	100 24.8 7.8	100 35.4 3.8	100 1.29 0.73	100 1.78 0.94	3	7
Rattlesnake Creek Upper-BLM	2.4	96.8	21 45.4 18.1	12 85.1 11.9	21 15.7 6.3	12 30.9 2.8	21 1.12 0.44	12 2.00 1.45	0	17
Rattlesnake Creek Lower-BLM	4.4	114.8	16 39.2 6.4	5 115.3 23.2	16 18.6 2.9	5 39.1 5.7	16 1.06 0.17	5 2.80 1.30	0	20
Mean	11.9	83.9	49.0	86.3[c]	21.2	34.7[c]	1.29	2.25[c]	2	15
Standard Deviation	11.5	23.4	7.1	17.8	4.1	3.6	.21	.45		

[a]Values are Sample Size/Mean/Standard Deviation.

[b]Estimated following Keen (1943) as adapted by Keister and Anthony (1983).

[c]Mean for roost trees was significantly larger ($P < .05$) than mean for forest stand trees.

source of food (Steenhof *et al.* 1980). Changes in local food abundance may affect use of a particular communal roost. In the winter of 1982-83, the frozen carcasses of 39 cows drowned in Chickahominy Reservoir were available to scavengers from mid-January to early March. The Silver Creek roost received maximum use (24 eagles) during that time. In 1984, no cow carcasses were observed at Chickahominy Reservoir and only 3 eagles used the Silver Creek roost. The Silver Creek roost was the closest stand of large ponderosa pine trees (13.3 km north-northwest) to Chickahominy Reservoir.

During 1983 and 1984, use of deciduous tree roosts peaked in mid-to-late February, whereas use of conifer roosts peaked in mid-to-late March. Use of roosts in deciduous trees was highest during the most severe part of the winter and low in spring during the time of peak eagle numbers. We believe that factors other than weather (i.e. social behavior and/or food distribution) affected the differential use of coniferous and deciduous tree roosts. In contrast, Thompson and Littlefield (1983) reported greater use of conifer roosts during severe weather.

Roosting Habitat—Conifer stands used by bald eagles for communal roosting (n = 245) were mainly ponderosa pine (69%) with white fir (*Abies* spp. 16%), Douglas-fir (*Pseudotsuga menziesii* 15%), and trembling aspen (*Populus tremuloides* <1%) also present. All roost trees observed (N = 180) were >30.5 cm dbh and all were ponderosa pine except for one Douglas-fir. Roost size ranged from 2.4 to 28.3 ha, and tree density ranged from 53.7 to 114.8 trees/ha (Table 2). Roost trees were larger in diameter ($P < 0.005$), taller ($P < 0.05$), and had more open structure ($P < 0.05$) than the forest stand as a whole. In addition, the percentage of spike-

topped trees and snags was higher in the roost tree sample than in the stand sample (Table 2). These findings are similar to forest stand and roost tree characteristics described by Keister and Anthony (1983) in the Klamath Basin and summarized by Anthony *et al.* (1982) for communal roosts throughout the Pacific Northwest. Also, the dbh of 98% of roost trees sampled in the Harney Basin was larger than the minimum old-growth specifications (53.3 cm dbh) established by the USDA Forest Service (1981) for the ponderosa pine forest type.

Communal roosts and similar stands should be managed to maintain old-aged trees in an uneven-aged stand condition (Anthony *et al.* 1982). Roosts in deciduous trees were closer to the principal feeding areas and should be preserved or enhanced by plantings. Major changes in the hydrology of the basin should be avoided because channelization, stabilization, or any management activity that results in drastic changes in seasonal flooding could affect the use of the area by waterfowl and eagles. Ranchers should be encouraged to leave cow carcasses in areas available to eagles and away from human activity.

Acknowledgments

Funding was provided by the Bureau of Land Management and USDA Forest Service with additional support from the Oregon Department of Fish and Wildlife and U.S. Fish and Wildlife Service. We thank F. Taylor, A. Archie, M. Archie, J. Lemos, G. Gunderson, K. Klatt, G. Keister, S. Thompson, D. Paullin, G. Ivey, G. Sheeter, M. St. Louis, B. Reimers, J. Farsvedt, A. Polenz, R. Garner, C. Geisler, B. Anderson, C. Bacon, B. Ehlers, R. Opp, N. Taylor, C. Littlefield, F. McDonald, L. Klatt, and Boy Scout Troop 441, Burns, Oregon, for assisting in data collection. We extend a very sepcial thanks to G. Keister for sharing his insight and experience and to D. Anderson for his able field assistance. J. Crawford, G. Keister, R. Anderson, A. Bruce, R. Goggans, and two anonymous reviewers offered constructive comments on earlier drafts of this manuscript. This study was conducted under the auspices of the Oregon Cooperative Wildlife Research Unit; Oregon State University, Oregon Department of Fish and Wildlife, U.S. Fish and Wildlife Service, and the Wildlife Management Institute cooperating. This is Oregon State University Agricultural Experiment Station Technical Paper No. 7633.

Literature Cited

Anthony, R. G., R. L. Knight, G. T. Allen, B. R. McClelland, and J. I. Hodges. 1982. Habitat use by nesting and roosting bald eagles in the Pacific Northwest. Trans. N. Amer. Wildl. Nat. Res. Conf. 47:332-342.

Beck, D. L. 1980. Wintering bald eagles in the Wells Resource Area, Elko District, Nevada; 1979-80. U.S. Dept. Inter., Bur. Land Manage., Elko Dist., Nevada.

Edwards, C. C. 1969. Winter behavior and population dynamics of American eagles in western Utah. Brigham Young University, Provo. Thesis.

Franklin, J. R., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA, Forest Serv., Gen. Tech. Rep. PNW-8. Pac. Northw. For. Range Exp. Sta., Portland, Oregon.

Keen, F. P. 1943. Ponderosa pine tree classes redefined. J. For. 41:249-253.

Keister, G. P., and R. G. Anthony. 1983. Characteristics of bald eagle communal roosts in the Klamath Basin, Oregon and California. J. Wildl. Manage. 47:1072-1079.

Keister, G. P., Jr., R. G. Anthony and E. J. O'Neill. 1987. Use of communal roosts and foraging areas by bald eagles wintering in the Klamath Basin. J. Wildl. Manage. 51:413-418.

Malheur National Wildlife Refuge. 1939-1982. Narrative reports. Malheur Wildlife Refuge files, Refuge Headquarters, Burns, Oregon.

McClelland, B. R., L. S. Young, D. S. Shea, P. T. McClelland, H. L. Allen, and E. B. Spettigue. 1982. The bald eagle concentration in Glacier National Park, Montana: Origin, growth, and variation in numbers. The Living Bird 19:133-155.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, Inc., New York.

Paullin, D. G., and C. D. Littlefield. 1977. Malheur-Harney Lakes Basin study, Oregon report No. 1: A summary of biological data for calendar years 1975-1976. U.S. Dept. Inter., Fish and Wildl. Serv., Portland, Oregon.

Platt, J. B. 1976. Bald eagles wintering in a Utah desert. American Birds 30:783-788.

Reynolds, T. D., N. D. Ertter, D. K. Broemeling, and R. P. Howard. 1985. Winter distribution of bald eagles along a segment of the Boise River, Idaho. Northw. Sci. 59:93-96.

Steenhof, K., S. S. Berlinger, and L. H. Fredrickson. 1980. Habitat use by wintering bald eagles in South Dakota. J. Wildl. Manage. 44:798-805.

Thompson, S. P., and C. D. Littlefield. 1983. Bald eagles in the Malheur-Harney Lakes Basin, southeast Oregon: History and current status. Unpublished report. Malheur Nat. Wildl. Ref., Burns, Oregon.

USDA Forest Service. 1981. Pacific Northwest Regional Plan Draft. USDA, Forest Service, Portland, Oregon.

U.S. Dept. Commerce. 1981. Local climatological data. Burns, Oregon. National Climatic Center, Asheville, North Carolina.

U.S. Dept. Interior. 1978. Determination of certain bald eagle populations as endangered or threatened. Fed. Reg. 43:6230-6233.

Walter, H., and K. L. Garrett. 1981. The effects of human activity on wintering bald eagles in the Big Bear Valley, California: Final report. Dept. Geography, Univ. Calif., Los Angeles.

Young, L. S. 1983. Movements of bald eagles associated with autumn concentrations in Glacier National Park. University of Montana, Missoula. Thesis.

Received 3 February 1986
Accepted for publication 9 October 1986

George A. Liknes and **William R. Gould,** Montana Cooperative Fishery Research Unit[1]
Biology Department, Montana State University, Bozeman, Montana 59717

The Distribution, Habitat and Population Characteristics of Fluvial Arctic Grayling (*Thymallus arcticus*) in Montana

Abstract

The only substantial population of native stream dwelling Arctic grayling (*Thymallus arcticus*) in the lower 48 states is located in the upper Big Hole River drainage of Montana. This population, a taxon of special concern, is genetically different from any other Montana or Wyoming population in allele frequencies at variable loci. It represents a unique gene pool which should be preserved. In 1978 and 1979, Arctic grayling were found in three sections of the Big Hole River and in 11 tributary streams. Where Arctic grayling were most abundant, the mean water depth (standard deviation) was 28.4 (22.6) cm, mean width was 12.21 (4.92) m, mean velocity was 0.21 (0.15) m/s, and mean water temperature for the period 21 April to 1 September, 1979 was 13.7 (4.7)° C. In this area, the gradient was 0.29 percent, rubble and gravel comprised 85 percent of the substrate and total shoreline cover was approximately 262 m^2/km of stream.

Growth rates (mean increment of back-calculated length) of Arctic grayling within the study area were greatest (118 mm) during their first year of life and decreased to 23 mm between the 4th and 5th year. Arctic grayling reached sexual maturity at age three at which time they had a back-calculated length of 275 mm.

The core of the population was confined to the Big Hole River itself or the lower portions of tributaries above the mouth of the North Fork Big Hole River. This baseline information will allow future comparisons to asssess the population's status and insure that management actions beneficial to the population can be implemented when necessary. Because the range of this genetically distinctive population has dwindled over several decades, it may be endangered and suitable habitat sites should be identified to which Arctic grayling can be transplanted.

Introduction

At the turn of the century in the lower 48 United States, populations of fluvial Arctic grayling (*Thymallus arcticus*) occurred in northern Michigan and western Montana east of the continental divide and in a small portion of the upper Missouri River drainage within Yellowstone National Park, Wyoming. The Michigan form became extinct around 1936 (Scott and Crossman 1973) and in Montana, Arctic grayling that were widely but intermittently distributed in the Missouri River and its tributaries above the Great Falls (Vincent 1962, Henshall 1906) are now found only in the upper Big Hole River and its tributaries.

The greatly reduced range led to the designation of the fluvial Arctic grayling of Montana as a taxon of special concern by the Endangered Species Committee of the AFS (Deacon *et al.* 1979). Concern for the continued existence of this unique population in the upper Big Hole River drainage has recently increased. Only small numbers of Arctic grayling were found in previous sampling and new biological and physical factors may be impacting the population. Brown trout (*Salmo trutta*) and rainbow trout (*S. gairdneri*) may be pioneering the area and oil exploration has occurred in the drainage.

In this study we examined the distribution, habitat-use, and population characteristics of the relict population of stream-dwelling Arctic grayling in the upper Big Hole River to: (1) provide a database for monitoring the well-being of this unique gene pool and (2) identify Arctic grayling habitat characteristics so suitable areas outside the present range could be identified as areas for possible transplants.

Description of Study Area

The study area encompassed the upper Big Hole River drainage of southwestern Montana and contains tributaries from the Bitterroot and Anaconda Ranges and the Pioneer Mountains. It extended approximately 90 km from the headwaters of the Big Hole River to Sportsman Park (Figure 1). The Big Hole River flows in braided, meandering channels above Pintlar Creek (Figure 1) but is confined to a single channel by a narrow canyon below that point. Grasses, sedges, and willows were present on the extensively irrigated land adjacent to the river and conifers also were present in the riparian zone below Pintlar Creek.

[1]The Montana Cooperative Fishery Research Unit is jointly sponsored by the U.S. Fish & Wildlife Service, Montana Department of Fish, Wildlife and Parks, and Montana State University.

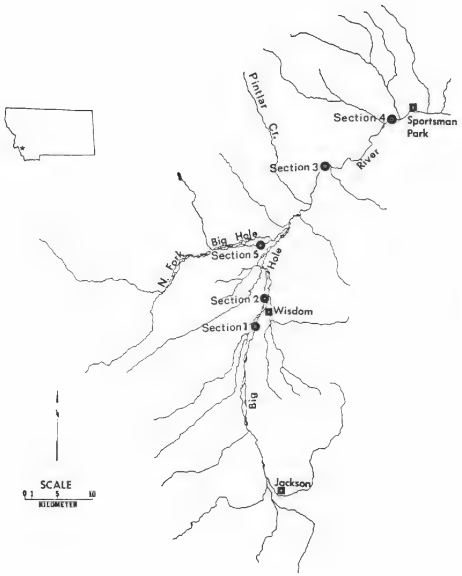

Figure 1. Map of study area showing locations of study sections.

A sagebrush-grassland vegetation type was present on the foothills surrounding the tributary streams.

The maximum and minimum recorded discharges at a site 15 km upstream of Jackson (Figure 1) from 1940-1954 was 26.56 m^3/s and 0.142 m^3/s, respectively (Aagaard 1969). During the first year of the study, the mean discharge at a site approximately 8 km downstream from Jackson was 4.4 m^3/s between 26 July and 15 September, 1978 (Wells and Rehwinkel 1980). National Oceanic and Atmospheric Administration (1977, 1978, and 1979) precipitation records at Wisdom (Figure 1) and summer flow measurements in 1979 indicate that discharges may have been up to 40% lower in 1979 than in 1978.

Methods

The distribution of fluvial Arctic grayling in the upper Big Hole River drainage was determined from collections made at numerous sites by angling and electrofishing for adults and juveniles; seining and drift nets were used to sample for larvae. Four sections on the river (3500-4900 m in length) and one on its principal tributary, the North Fork (2050 m in length), were electrofished to obtain fish population estimates (Figure 1). In areas of the river containing multiple channels, work was confined to the major channel.

Population estimates were calculated using Chapman's modification of the Petersen formula (Ricker 1975). Weights and total lengths of captured Arctic grayling were recorded and scales were taken from an area posterior of the dorsal fin above the lateral line for age-growth analysis. Back-calculated lengths of fish at each age were determined using Hile's (1941) modification of the Monastyrsky method. Predicted and mean weights at each age were computed using the logarithmic form of the standard length-weight relationship equation (Bagenal and Tesch 1978).

Physical habitat features of Sections 1, 2, and 3 were measured to correlate with Arctic grayling abundance. The length of each section, pool, and riffle were measured in the center of the channel. A pool-riffle periodicity (Leopold and Langbein 1966) and ratio were calculated for each section. Pools were defined as areas with reduced water velocities, smooth surfaces, and maximum depths $\geq$ 0.5 m. The remaining portions of the study sections were designated riffles. Gradients for each section were estimated using U.S. Geological Survey topographical maps.

In 1979, 37 transects were established perpendicular to the channel on each section where physical habitat data was gathered; distances between the transects on Sections 1-3 were 45, 100, and 150 m, respectively. Transects were located only on the upper half of Section 1 since the lower half was completely dewatered in 1979. However, the habitat in the upper portion of Section 1 appeared to be representative of the entire section. On each transect, water depth was recorded to the nearest 1 cm at intervals of 0.5 m. Velocities were measured to the nearest 0.003 m/sec at 1 m intervals in Sections 1 and 2 and at 3 m in Section 3 with a Gurley AA current meter. Discharge in each section was calculated from measurements of selected transects.

Shoreline or instream cover 1.5 m to each side of a line transect was measured to the nearest 0.01 m. Shoreline cover was defined as overhanging brush within 1.0 m of the water surface or debris and undercut banks within 0.6 m of the water surface. Instream cover included

both aquatic plants and debris. The general condition of banks at each transect was qualitatively evaluated as stable or unstable; unstable banks were defined as those showing recent soil erosion.

Substrate composition was determined by visually estimating the amount of each type of material along each transect. Bottom materials were classified after Wentworth (1922) as bedrock (unbroken, solid rock), boulders (>26.0 cm in diameter), rubble (6.4-26.0 cm in diameter), gravel (2.0 mm - 6.3 cm in diameter), and fines (<2.0 mm in diameter).

Water quality analysis at Sections 1, 2, 3, and 5 occurred bimonthly from 16 June-1 September, 1979. Dissolved oxygen concentrations were determined to the nearest 0.1 mg/l by the azide modification of the Winkler method (American Public Health Association 1976). Alkalinity and hardness were determined by titration with precision to 5 mg/l $CaCO_3$ and the specific electrical conductance was measured with a Beckman RB3-Solu Bridge to the nearest 0.5 μmhos/cm. The pH was determined in the field with an Orion model 407 Specific Ion Meter (resolution = 0.01 pH units). Water temperature was continually monitored to the nearest 0.5 C with Ryan model D-15 thermographs.

Statistical tests were performed according to methods in Snedecor and Cochran (1967) using MSUSTAT (Lund 1979) and SPSS (Nie *et al.* 1975). Values having probabilities of $p < 0.05$ were termed significantly different.

Results

Distribution and Abundance

Arctic grayling were collected at seven locations on the main river and from 11 tributary streams (Figure 2). Fry or young of the year (yoy) were collected at 14 points, 1+ and older fish at four locations and fry and 1+ and older fish together at 12 sites. None were observed in Deep, Warm Springs, Johnson or Fishtrap creeks. Johnson Creek is a tributary of the North Fork Big Hole River.

The relative abundance of Arctic grayling was greatest in Section 1. The average number of Arctic grayling 81-335 mm in total length captured per kilometer on each electrofishing run in Sections 1, 2, and 5 were 16.9, 5.3, and 4.9, respectively. No Arctic grayling were obtained in Sections 3 and 4. In Section 1, the number and standing crop (80 percent confidence intervals) of

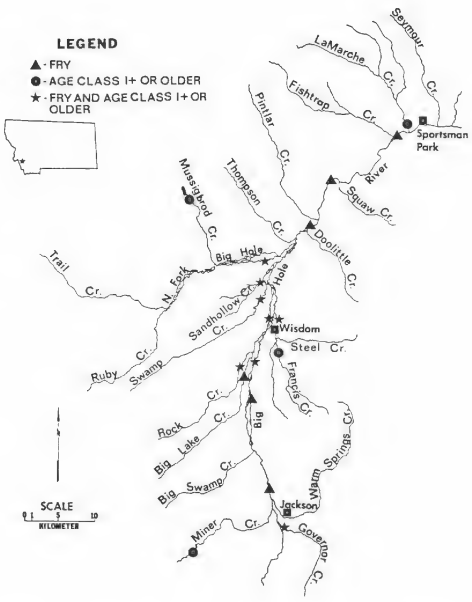

Figure 2. Collection sites of Arctic grayling in the upper Big Hole River drainage, 1978-79.

Arctic grayling 251-297 mm in total length were 35 (±11)/km and 6.7 (±2.5) kg/km or 28 (±9)/hec and 5.5 (±2) kg/hec, resepctively. Population estimates were not obtained in any other section.

Age, Growth, and Spawning

Back-calculated lengths and weights of Arctic grayling from locations throughout the upper Big Hole River drainage were similar, so all the data were combined (Table 1). Their growth rate was most rapid the first year and displayed a pronounced decline between the second and third years. Arctic grayling in the upper Big Hole River attained sexual maturity at age three when their back-calculated length was 275 mm.

The largest number of Arctic grayling captured were obtained in July and August, 1978; these 312 fish allowed us to examine the population's size structure. The dominant age groups were two and three, comprising 47.1 and 30.4 percent of the sample, respectively. Young of the year represented only 7.7 percent of these fish; however, this is due to bias of sampling gear which is more efficient capturing age one and

TABLE 1. Mean total length and weight (standard deviation in parentheses) at time of capture and calculated mean total length and weight at each annulus for Arctic grayling Age 1+ and older captured in the upper Big Hole River drainage in 1978 and 1979.

Age Group	N	Mean total length (mm)	Mean total weight (gm)	Calculated length (mm) at age				
				1	2	3	4	5
1	61	198 (20)	76 (23)	116				
2	190	261 (16)	168 (34)	119	221			
3	167	292 (19)	231 (45)	117	223	275		
4	12	316 (22)	282 (56)	119	230	278	305	
5	1	381	431	150	272	320	356	379
Mean back-calculated length (mm)				118	222	275	309	379
Mean increment of back-calculated length (mm)				118	104	52	28	23
Calculated weight (gm)				27	115	188	247	395

older fish. Age one fish also made up a relatively low portion of the sample, 12.2 percent. Age class four was represented by only 8 individuals (2.6 percent).

Most spawning activity in the Big Hole River during 1979 occurred in late April and early May. A total of 146 age 0 Arctic grayling were collected throughout the upper Big Hole River drainage from 27 May-27 July, 1979. The mean total length of yoy increased from 12.2 mm during 27-31 May to 55.2 mm for the period 11-15 July. Some fry apparently left the spawning streams and moved into the main river shortly after hatching, while others remained much longer, even in intermittent streams such as Sandhollow Creek (Figure 2). Most yoy Arctic grayling captured moving out of Sandhollow Creek were obtained from overnight drift net sets.

Sympatric species

Eleven species of fish coexisted with Arctic grayling in the study area. Mountain whitefish (*Prosopium williamsoni*) and brook trout (*Salvelinus fontinalis*) were the most abundant game fish present throughout the study area. Longnose suckers (*Catostomus catostomus*), burbot (*Lota lota*), mottled sculpin (*Cottus bairdi*), longnose dace (*Rhinichthys cataractae*), rainbow trout (*Salmo gairdneri*), cutthroat trout (*S. clarki*) and rainbow-cutthroat trout hybrids (*S. gairdneri* X *S. clarki*) were also found in the study area. Only one brown trout (*S. trutta*) was collected during this study. Brook, rainbow and brown trout are introduced species in Montana. Also, mountain (*C. platyrhynchus*) and white suckers (*C. commersoni*) have been reported to inhabit the area (Wells and Rehwinkel 1980), but none were observed during this investigation.

Habitat Characteristics

Stream Morphology and Cover

Morphological measurements made on Sections 1-3 showed that mean, pool, and riffle width increased in a downstream direction (Table 2). Analysis of variance showed significant differences in some habitat parameters between the sections. Comparison of sample means (Q test; $P < 0.05$) showed that Section 1, with the greatest density of Arctic grayling, was significantly narrower than Section 3, significantly shallower than Sections 2 and 3, and had a significantly slower mean thalweg velocity than Section 2. Also, the percentage of stable banks and the pool-riffle periodicity were lower than in the two downstream sections. The pool-riffle ratio was greatest in Section 1 and decreased in a downstream direction through the study sections, as did the gradient. The composition of bottom materials in all three sections were similar, consisting primarily of rubble and gravel. The area of shoreline and instream cover per kilometer in

TABLE 2. Mean values and standard deviations (in parentheses) of physical habitat parameters measured in study sections on the upper Big Hole River between 16 July and 20 August, 1979.

Parameter	Section 1	Section 2	Section 3
Width (m)	12.21(4.92)	15.95(5.02)	48.09(14.75)
Riffle width (m)	10.83(4.77)	12.62(4.46)	51.50(15.81)
Pool width (m)	8.95(5.23)	13.40(5.30)	40.00(7.60)
Thalweg depth (cm)	54.7(24.0)	77.3(33.5)	61.8(22.0)
Depth (cm)	28.4(22.6)	39.7(30.6)	37.3(23.1)
Thalweg velocity (m/s)	0.27(0.18)	0.42(0.28)	0.32(0.15)
Velocity (m/s)	0.21(0.15)	0.33(0.23)	0.21(0.15)
Stable banks (%)	70.3(5.0)	78.4(4.8)	93.2(2.9)
Pool-riffle periodicity	6.3(4.2)	7.2(4.5)	11.6(7.6)
Pool-riffle ratio	1.51	1.29	0.27
Gradient (%)	0.29	0.23	0.11
Flow (m^3/s)	0.68	2.07	3.50
Bottom materials (%)			
Boulders	0.9(5.5)	0.0	0.1(0.8)
Rubble	41.5(19.8)	38.8(14.2)	51.4(15.6)
Gravel	42.8(16.2)	39.3(12.9)	33.0(11.3)
Fines	14.8(17.7)	21.9(20.3)	15.5(15.5)
Shoreline cover (m^2/km)	261.4	456.2	8.4
Instream cover (m^2/km)	51.0	92.8	0.0

Section 1 was 57 and 55 percent of those respective features in Section 2. Both shoreline and instream cover were virtually absent in Section 3.

Water Temperature and Quality

Analysis of variance on water temperatures of Sections 1-3 showed significant differences. The mean water temperature (Table 3) in Section 1 was similar to that in Section 2, but significantly lower than in Section 3 (Q test; $P<0.05$). Mean water temperatures in Sections 1 and 2 were also significantly lower than in Section 5 for comparable periods of time (Q test; $P<0.05$). The recorded number of hours water temperatures exceeded 17° C was similar in both Sections 1 (895) and 2 (727), and was significantly lower than in Section 3 (1342) for comparable periods of time (Chi square; $P<0.05$). More hours of water temperatures above 17° C were recorded in July than any other month. During this month, temperatures were above 17° C about 60, 60, and 83 percent of the time on Sections 1, 2, and 3, respectively.

There were no significant differences among other parameters from any section on the main river (Table 3). The water in the upper Big Hole River was soft, its pH was nearly neutral, it had a fairly low capacity to neutralize acids and had a low electrical conductance. Mean values of dissolved oxygen were similar throughout the study area. Each individual value was above 85 percent and mean values were all >100 percent saturation. Data from Section 5 on the North Fork showed that the principal tributary had lower mean alkalinity, hardness and conductivity values than the main river.

Discussion

Virtually all of the fluvial Arctic grayling collected during this study were from locations in the Big Hole River itself or from sites in tributaries near the river. The only Arctic grayling found far upstream in tributaries were in Miner and Mussigbrod creeks. They were captured upstream and downstream, respectively, from lacustrine populations and probably do not represent portions of the fluvial population. Furthermore, the core of the Arctic grayling population was located in the drainage above the mouth of the North Fork Big Hole River. Twelve collections (excluding those from Miner and Mussigbrod creeks) were made in this area, while only four collections were made below this point. However, in previous years, Arctic grayling have also been found at sites below the North Fork (Peterson 1974, Wells and Rehwinkel 1980) and individuals have appeared as far as 85 km downstream from the study area. (J. Wells, Montana Department of Fish, Wildlife and Parks, Bozeman, MT, personal communication).

The relative abundance of Arctic grayling also was greater upstream from the mouth of the North Fork. In this study, densities above the North Fork were about 5-17 fish/km per electrofishing run, while those below were 0 fish/km in the study area and 0.6-2.8 Arctic grayling per electrofishing run/km in other surveys (Peterson 1974, Wells and Rehwinkel 1980).

Summer water temperatures may be an important limiting factor for Arctic grayling in the

TABLE 3. Mean and ranges (in parentheses) of water quality parameters and temperatures from study sections on the upper Big Hole River, 21 April-1 September, 1979.

Parameter	Section			
	1	2	3	5
Temperature (°C)	13.7 (0-24)	13.6 (1-25)	15.2 (2-25)	18.0* (12.5-23)
Total alkalinity (mg/l $CaCO_3$)	51 (35-60)	51 (40-60)	56 (35-70)	37 (30-40)
Total hardness (mg/l $CaCO_3$)	43 (40-50)	41 (40-50)	36 (30-45)	26 (15-30)
Calcium hardness (mg/l $CaCO_3$)	32 (25-40)	34 (30-40)	30 (20-40)	22 (15-30)
Magnesium hardness (mg/l $CaCO_3$)	11 (0-20)	7 (0-10)	6 (0-10)	3 (0-10)
pH	7.44 (7.22-7.64)	7.38 (6.78-7.80)	7.56 (7.26-7.72)	7.24 (7.04-7.38)
Conductivity (μmhos/cm)	94.1 (50-120)	100.3 (52.5-120)	105.8 (52.5-140)	71.7 (55-90)
Dissolved oxygen (mg/l)	8.7 (7.7-10.2)	8.7 (7.6-10.3)	8.8 (6.5-11.6)	8.8 (7.9-10.0)

*Based on data collected from 23 June-25 August, 1979.

river downstream of the North Fork. Although the thermal tolerance of Arctic grayling is not precisely known, Vincent (1962) reported that the range of temperature tolerance for Arctic grayling was usually between 10 and 18.3° C. Furthermore, water temperatures of 17 ° C and above exceed the physiological optimum for growth and food conversion efficiency of salmonids (Brett *et al.* 1969, Wurtsbaugh and Davis 1977). The high summer water temperatures measured in the lower portion of the study area may have been largely responsible for the absence of adult Arctic grayling there during this study.

Arctic grayling in the upper Big Hole drainage underwent rapid growth during the first two years of life with a large reduction between the second and third, which was similar to that of Arctic grayling from the Red Rock drainage (Nelson 1954). However, their growth rates were less than those in two other Montana streams outside the Big Hole drainage (Peters 1964). The minimum age and back-calculated length at sexual maturity for individuals found during this study was three years and 275 mm, respectively. In other Montana populations, a few individuals have been reported to mature at age two (Lund 1974, Peterman 1972, Nelson 1954, Brown 1938) while in the northern portion of their range, Arctic grayling usually reach sexual maturity between age four and six (Bishop 1971, Wojcik 1955). The minimum length at maturity was similar to the 270 mm length suggested by Wojcik (1955) for Alaskan Arctic grayling.

Reverse Lee's phenomenon is present in the back-calculated lengths. Older fish have a larger calculated length for a given age than younger fish at the same age. Possible causes of this include incorrect back-calculation or scale reading procedures, non-random sampling of the stock, and selective natural mortality that affects smaller fish in a particular age group more. Such natural mortality may result from either interspecific or intraspecific competition.

Management Applications

The data obtained on the distribution, relative abundance, and biological parameters of Arctic grayling in the upper Big Hole River provide baseline information for future comparisons. Any significant and persistent decrease in range, relative numbers, growth rates or increase in age at sexual maturity should be a stimulus for additional and immediate management action on this population, which has been determined to be genetically different than any other Montana

or Wyoming population sampled to date in allele frequencies at variable loci (Everett and Allendorf 1985).

One of the most pressing management actions needed to be addressed is the identification of suitable habitat sites outside the Big Hole River for transplants from this unique population. In that portion of the river where Arctic grayling were most abundant, the mean depth (standard deviation) was 28.4 (22.6) cm, mean width was 12.21 (4.92) m, mean velocity was 0.21 (0.15) m/s, mean water temperature for the period 21 April to 1 September, 1979 was 13.7° C, and the maximum water temperature was 24° C. In this area, the gradient was 0.29 percent, rubble and gravel comprised 85 percent of the substrate and total shoreline cover was approximately 261 m^2/km of stream. Transplant sites having similar physical habitat characteristics to these should be sought, while areas more like Section 3 should be considered less desirable. However, since yoy Arctic grayling were found in the river near Section 3, is should be considered suitable habitat for use at some point in their life history.

The presence of other fish at the potential transplant sites is another factor which must be considered. Sites with only cutthroat trout and mountain whitefish should receive highest priority since Arctic grayling evolved in sympatry with these species. Competition with introduced fish has often been suggested as a major reason for the reduction in the Arctic grayling's range in Montana and Michigan. While this may be accurate, the competitive interactions responsible for the Arctic grayling's decline have not been identified. The possibility that non-native fish simply replaced Arctic grayling populations depressed by other factors should be investigated. Vincent (1962) believed that interspecific competition with exotics would manifest itself in 40 years. However, brook trout were introduced into the upper Big Hole drainage around 1929 and have not eliminated the Arctic grayling. Perhaps this portion of the river is optimal habitat for Arctic grayling and they have thus been able to hold their own against the introduced competitors. Nevertheless, this indicates suitable locations with brook trout also might be considered, although as less desirable sites.

References Cited

Aagaard, F. C. 1969. Temperature of surface waters in Montana. U.S. Geol. Survey and Montana Fish Game Comm.

American Public Health Association. 1976. Standard methods for the examination of water and wastewater, 14 ed. Amer. Pub. Health Assn., Washington, D.C.

Bagenal, T. B., and F. W. Tesch. 1978. Age and growth. *In* T. B. Bagenal (ed.). Methods of assessment of fish production in fresh waters, 3 ed. Blackwell Sci. Pub., Oxford and Edinburgh, Great Britain. Pp. 101-136.

Bishop, F. G. 1971. Observations on spawning habits of the Arctic grayling. Prog. Fish Cult. 33:12-19.

Brett, J. R., J. E. Shelbourn, and C. T. Shoop. 1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka,* in relation to temperature and ration size. J. Fish. Res. Bd. Can. 26:2363-2394.

Brown, C. J. D. 1938. Observations on the life history and breeding habits of the Montana grayling. Copeia 1938:123-126.

Deacon, J. E., G. Kobetich, J. D. Williams, S. Contreras, and other members of the Endangered Species Committee of the American Fisheries Society. 1979. Fishes of North America endangered, threatened or of special concern: 1979. Fisheries 4:29-44.

Everett, R. J., and F. W. Allendorf. 1985. Population genetics of Arctic grayling: Grebe Lake, Yellowstone National Park. Pop. Gen. Lab. Rep. 85/1, University of Montana.

Henshall, J. A. 1906. A list of the fishes of Montana. Bull. Univ. Mont. 34:1-12.

Hile, R. 1941. Age and growth of the rock bass, *Ambloplites rupestris* (Rafinesque), in Nebish Lake, Wisconsin. Trans. Wis. Acad. Sci. Arts. Lett. 33:189-337.

Leopold, L. B., and W. B. Langbein. 1966. River meanders. Sci. Amer. 214:60-70.

Lund, J. A. 1974. The reproduction of salmonids in the inlets of Elk Lake, Montana. Montana State University. Thesis.

Lund, R. E. 1979. A user's guide to MSUSTAT—an interactive statistical analysis package. Dept. Math. Sci. Montana State University.

National Oceanic and Atmospheric Administration. 1977. Climatological Data: Montana. 80:5-8.

_____. 1978. Climatological Data: Montana. 81:5-8.

_____. 1979. Climatological Data: Montana. 82:5-8.

Nelson, P. H. 1954. Life history and management of the American grayling (*Thymallus signifer tricolor*) in Montana. J. Wild. Mgmt. 18:324-342.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. Statistical package for the social sciences, 2 ed. McGraw-Hill, Inc., New York.

Peterman, L. G. 1972. The biology and population characteristics of the Arctic grayling in Lake Agnes, Montana. Montana State University. Thesis.

Peters, J. C. 1964. Age and growth studies and analysis of bottom samples in connection with pollution studies. Fed. Aid Proj. F-23-R-6, Job. no. I and II. Mont. Dept. Fish Game, Helena.

Peterson, N. 1974. Southwestern Montana Fisheries Study. Fed. Aid Proj. F-9-R-22, Job. no. I-b. Mont. Dept. Fish Game, Helena.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Dept. Env., Fish Mar. Serv. Bull. 191. Ottawa, Canada.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fish. Res. Bd. Can. Bull. 1984. Ottawa, Canada.

Snedecor, G. W., and W. G. Cochran. 1967. Statistical methods, 6 ed. Iowa St. Univ. Press, Ames.

Vincent, R. E. 1962. Biogeographical and ecological factors contributing to the decline of Arctic grayling, *Thymallus arcticus* (Pallas), in Michigan and Montana. University of Michigan. Dissertation.

Wells, J. D., and B. J. Rehwinkel. 1980. Southwest Montana fisheries study. Fed. Aid Proj. F-9-R27, Job. no. I-b. Mont. Dept. Fish Wild. Parks, Helena.

Wentworth, C. K. 1922. Grades and class terms for clastic sediments. J. Geol. 30:377-392.

Wojcik, F. J. 1955. Life history and management of the grayling in interior Alaska. University of Alaska, Fairbanks. Thesis.

Wurtsbaugh, W. A., and G. E. Davis. 1977. Effects of temperature and ration level on the growth and food conversion efficiency of *Salmo gairdneri,* Richardson. J. Fish Biol. 11:87-98.

Received 9 April 1986
Accepted for publication 5 November 1986

Review Article

Sherman A. Minton, Department of Microbiology and Immunology
Indiana University School of Medicine
Indianapolis, Indiana 46223

Poisonous Snakes and Snakebite in the U.S.: A Brief Review

Abstract

This article briefly reviews some current ideas regarding snakebite in the United States. Twenty species of native venomous snakes occur and include 15 species of rattlesnakes, the copperhead and cottonmouth, two species of coral snakes, and one seasnake. Snake venoms contain a variety of enzymes and non-enzymatic toxins. Composition may vary geographically, ontogenetically, and individually. As determined by mouse toxicity, most lethal venoms are those of the Mohave rattlesnake (*Crotalus scutulatus*), tiger rattlesnake (*C. tigris*), and pelagic seasnake (*Pelamis platurus*). Venomous snakes may bite without injecting venom and rarely inject more than half their available venom. Some colubrid snakes generally presumed nonvenomous, such as garter snakes, can in rare instances inflict venomous bites.

Most snakebites in the United States are sustained close to the victim's home and usually reach medical aid within an hour. Fishermen, hunters, and backpackers do not seem to be a high risk group. Almost half the bites result from deliberate contact with a venomous snake. Symptoms of pit viper envenomation are reviewed. A persistent drop in blood pressure is the single most reliable indication of dangerous envenomation. About half the coral snake bites do not result in envenomation, but it is serious when it occurs.

Snakebite first aid measures and principles of treatment are reviewed. Two relatively new procedures, elastic bandaging of a bitten limb and use of a powerful small suction device are discussed. Procedures under development include ELISA tests to improve diagnosis and evaluate therapy, antivenoms of higher potency and lower allergenicity, and immunization for high risk individuals. Because of the complexity of evaluating snakebite and the chance that a layman might attempt a naive treatment more harmful than helpful, the emphasis in first aid for snakebite is to get the stricken individual promptly to a hospital.

Introduction

Although venomous snakebites are uncommon in the United States (6000-7000 cases annually), they generate a disporportionate amount of interest, anxiety, and controversy. There are several reasons for this. First, snakebite is a situation where a complex organism (a snake) injects a complex secretion (venom) into another complex organism (a human). This generates a staggering number of variables and allows for outcomes that can range from death in less than an hour to a totally trivial injury. Second, the composition and amount of venom a snake injects varies with geographic locality, season, and the age, size, and health of the reptile. Third, there are no good animal models (aside from monkeys) for evaluating the action of snake venoms on man and the effectiveness of treatments. The mouse is widely used, but it is not a very small human being. Finally, the unpredictable course of snakebite and the limited knowledge that most physicians have of venomous snakes and their bites may cause uncritical acceptance of treatment plans.

The Snakes and Their Venoms

There are 20 species of unquestionably venomous snakes known from the United States—15 species of rattlesnakes, the copperhead and cottonmouth, two other pit vipers that are closely related to each other, and two species of coral snakes. The pelagic seasnake (*Pelamis platurus*) is occasionally reported in Hawaiian waters and has been recorded once on the coast of extreme southern California. Additionally there are several snake species that are essentially harmless but can, on rare occasions, inflict a mildly venomous bite. Rattlesnakes occur in at least 45 of the contiguous states and four Canadian provinces, although they are usually quite local in distribution, and their numbers have been greatly reduced in the last half century. Species that present the greatest danger to man are the eastern and western diamondbacks (*Crotalus adamanteus* and *C. atrox*), timber rattlesnake (*C. horridus*), prairie rattlesnake (*C.v. viridis*), northern and southern Pacific rattlesnakes (*C.v. oreganus* and *C.v. helleri*), and Mohave rattlesnake (*C. scutulatus*). The pigmy rattlesnake (*Sistrurus miliarius*) causes many bites in the southern states, but

fatalities are unknown. The other species (see Table 1) either are uncommon or occur in regions where they have little contact with man. The copperhead (*Agkistrodon contortrix*), with a wide range in the eastern United States and ability to survive in well populated areas, probably causes more bites than any one species of rattlesnake, but fatalities are virtually unknown. The cottonmouth (*A. piscivorus*) has a more limited range and prefers swamps and sluggish waterways. Nevertheless it accounts for a significant number of snakebites in the southeastern states and fatalities are on record. Coral snakes are highly secretive and seldom seen. The eastern species (*Micrurus fulvius*), which may reach 1.2 m in length, is potentially lethal; the smaller Arizona species (*Micruroides euryxanthus*) has never caused a human fatality.

TABLE 1. Venomous snakes of the United States and Canada and their geographic distribution.

Scientific Name	Common Name(s)	Distribution
Crotalus adamanteus	Eastern Diamondback Rattlesnake	Coastal plain, from se. North Carolina to Louisiana
Crotalus atrox	Western Diamondback Rattlesnake	Western Arkansas & s. Oklahoma thru most of Texas to se. California*
Crotalus cerastes	Sidewinder	Southern Arizona & s. California deserts*
Crotalus horridus	Timber Rattlesnake Canebrake Rattlesnake (southern populations)	New England to n. Florida, west to central Texas, north to se. Nebraska, s. Wisconsin & se. Minnesota
Crotalus lepidus	Rock Rattlesnake	Mountains and canyons from s. central Texas to se. Arizona*
Crotalus mitchelli	Speckled Rattlesnake Panamint Rattlesnake	Western Arizona, se. Utah, s. Nevada, s. California*
Crotalus molossus	Blacktail Rattlesnake	South central Texas to w. Arizona*
Crotalus pricei	Twin-spotted Rattlesnake	Mountains of se. Arizona*
Crotalus ruber	Red Diamond Rattlesnake	Southwestern California*
Crotalus scutulatus	Mohave Rattlesnake	Trans-Pecos Texas to s. Nevada & adjacent California*
Crotalus tigris	Tiger Rattlesnake	South central Arizona*
Crotalus v. viridis	Prairie Rattlesnake	West Texas and New Mexico north to w. North Dakota, Montana, se. Saskatchewan & adjacent Alberta*
Crotalus v. helleri *C.v. oreganus*	Pacific Rattlesnake	Most of California north to s. central British Columbia*
Crotalus v. lutosus	Great Basin Rattlesnake	Nevada, w. Utah & Oregon, s. Idaho**
Crotalus willardi	Ridge-nosed Rattlesnake	Mountains of se. Arizona & adjacent New Mexico*
Sistrurus catenatus	Massasauga Rattlesnake	Southern Ontario, w. New York & nw. Pennsylvania southwest to se. Arizona & s. Texas*
Sistrurus miliarius	Pygmy Rattlesnake	Eastern North Carolina to e. Texas & Oklahoma, s. Missouri, sw. Kentucky
Agkistrodon contortrix	Copperhead	Southern New England to Florida panhandle, west to Trans-Pecos Texas, north to se. Nebraska, central Indiana & Ohio
Agkistrodon piscivorus	Cottonmouth Water Moccasin	Southeastern Virginia to central Texas mostly at low elevations, north to central Missouri & sw. Indiana
Micrurus fulvius	North American Coral Snake	Coastal plain from se. North Carolina to sw. Texas, north to sw. Arkansas*
Micruroides euryxanthus	Arizona or Sonora Coral Snake	Southern Arizona & sw. New Mexico*
Pelamis platurus	Pelagic Sea Snake Yellow-bellied sea snake	Hawaii, extreme sw. California coast. Few records, probably based on strays.*

*Species also occurs in Mexico.

**Other subspecies of *Crotalus viridis* occur in parts of Arizona, Utah, Colorado and Wyoming. These are *C.v. concolor* (Midget Faded Rattlesnake), *C.v. nuntius* (Hopi Rattlesnake), *C.v. cerberus* (Arizona Black Rattlesnake), and *C.v. abyssus* (Grand Canyon Rattlesnake).

Snake venoms are the most complex of animal toxins, containing up to twenty or so biologically active proteins and polypeptides. Many are enzymes. Those that are most important and widespread include phospholipase A and proteases (endopeptidases) that account for some of the hemorrhagic and necrotizing activity, arginine ester hydrolases that contribute to hypotensive and anticoagulant activity, and hyaluronidase that facilitates the spread of venom in tissues. There are also non-enzymatic myotoxins and neurotoxins. It must be emphasized, however, that the effects of snake envenomation result from many venom components acting in concert. The classification of venoms as neurotoxic, hemorrhagic, or myotoxic is usually an oversimplification.

As judged by mouse toxicity, the most lethal rattlesnake venom is that of the tiger rattlesnake (*Crotalus tigris*) followed by that of the Brazilian rattlesnake (*C. durissus terrificus*), Mohave rattlesnake, and midget faded rattlesnake (*C. viridis concolor*). All these venoms contain a powerful neurotoxin. In South American rattlesnakes, it is known as crotoxin; in North American rattlesnakes as Mohave toxin. Recent work shows the two are immunologically very similar (Weinstein *et al.* 1985). Mouse lethal doses for some rattlesnake and other snake venoms are shown in Table 2. Venoms of many snake species show individual, ontogenic, and geographic variation in lethality and other properties. Venoms of two gravid timber rattlesnakes collected the same day on the same hilltop showed a five-fold difference in lethal toxicity (Minton 1953). In at least three rattlesnake species, venoms of young snakes differ markedly from those of adults in protein composition (Minton 1967, Fiero *et al.* 1972, Minton & Weinstein 1986). In all, lethality seems to peak in snakes 6-9 months of age, then decline to adult levels. Reports of unexpectedly severe reactions to bites of young rattlesnakes indicate this variation may be of clinical significance (Reid & Theakston 1978). Over a large part of its Arizona range, venom of the Mohave rattlesnake does not contain Mohave toxin and is much like venom of the western diamondback rattlesnake in lethality and proteolytic and hemorrhagic activity (Glenn *et al.* 1983). Venom from western diamondback rattlesnakes from west Texas and Arizona has greater lethality but lower proteolytic activity than that of snakes from north Texas and Oklahoma (Minton & Weinstein 1986).

TABLE 2. Venom yields from adult snakes of average size and mouse lethal doses. Based chiefly on data from the author's laboratory and from Glenn & Straight (1982).

Species	Average Venom Yield (mg)	Mouse LD/50 mg/kg intra-venous	Mouse LD/50 mg/kg sub-cutaneous
Crotalus adamanteus	250-500	1.68	14.55
Crotalus atrox (NE)	200-400	3.15	19.52
Crotalus atrox (SW)	100-250	2.07	14.16
Crotalus cerastes	30-60	2.25	12.35
Crotalus horridus	100-200	2.63	9.15
Crotalus lepidus	5-30		11.55[1]
Crotalus mitchelli	75-150		10.90[2]
Crotalus molossus	150-300		16.42
Crotalus pricei	2-12	0.95	11.39
Crotalus ruber	200-400	3.72	21.25
Crotalus scutulatus	40-100	0.16	0.31[3]
Crotalus tigris	5-15	0.06	0.21
Crotalus v. viridis	50-100	1.61	16.15
Crotalus v. helleri	75-150	1.29	3.56
Crotalus v. concolor	10-25	0.28	
Crotalus willardi	2-15	1.61	
Sistrurus catenatus	15-40	0.25	5.25[4]
Sistrurus miliarius	7-25	3.65	24.25
Agkistrodon contortrix	40-70	10.92	25.60
Agkistrodon piscivorus	100-150	5.11	25.80
Micrurus fulvius	4-16	0.38	1.30
Micruroides euryxanthus	0.5-3	0.90	
Pelamis platurus	0.25-1		0.70[5]

[1]Based on specimens from the Big Bend region of Texas. Evidence indicates much variation in toxicity among populations of this species.

[2]Based on specimens from San Diego Co., California. A subspecies with much more toxic venom occurs in Baja California.

[3]Based on specimens from populations whose venom contains Mohave toxin.

[4]Based on Indiana specimens. Venom of western populations appears to be less toxic.

[5]Based on specimens from the Coral Sea.

Who Gets Bitten and Why

Those whose work or recreation takes them outdoors and into remote areas often consider themselves at special risk from snakebite. Unless their activities include hunting snakes, this is not the case. Snakebite throughout the world is largely a matter of contact hours. The snake that bites you is most likely one that lives in your garden or under your house. Most snakebites in the United States, unless they involve deliberate

contact with venomous snakes, occur within a half-mile of the victim's home. Writing of his extensive experience in California, Russell (1980 p. 269) says: "Contrary to popular opinion, most snakebites in the United States occur within a short distance from medical care. In California, over 90 percent of the rattlesnake bites occur within city limits or within 2 miles of city limits in foothill area... Few bites occur in backpackers, serious hunters, or fishermen ... In the past 20 years, there has been only one backpacker in the Sierras of California, who I know of, who has been bitten by a rattlesnake, and this happened when he was changing a tire at the end of his hike."

Until about 1950, most snakebites in the United States were associated with what could broadly be called agricultural activities. When I was growing up in southern Indiana, the first snakebite of the season might occur with mushroom hunting in late April but was more likely to be associated with strawberry or blackberry picking in late May or June. Other bites were sustained while lifting rocks, clearing weeds or rubbish, or doing other chores about the farm. Today there are many fewer small farms where most of the work is done by hand, and there has been a great increase in large scale mechanized agriculture. On the other hand, there has also been a decided increase in permanent or seasonal rural living. Rural children ages 5-12 have always been a comparatively high risk group if they live where venomous snakes are relatively plentiful. Children of this age are more likely to go barefoot and be less than careful where they step or where they put their hands. Many small children are insatiably curious about snakes and today are more likely to try to catch reptiles their grandparents at the same age would have killed forthright. Today a much higher percentage of bites involve deliberate contact with venomous snakes. Snake catching, snake handling, and the keeping of venomous snakes in captivity attract people whose motives vary from serious scientific interest to exhibitionism and religious fervor. With a few, abuse of alcohol and drugs may contribute to the risk.

The Bite and Its Effects

An important fact not always appreciated by physicians or laymen is that venomous snakes, including the most dangerous species, may inject little or no venom when they bite. According to one study, only about half the bites by the widely-feared Asian cobra result in poisoning (Reid 1964). In 16 of 31 coral snake bites in the southeastern U.S., no poisoning developed (Neill 1957, Parrish & Khan 1967). Rattlesnakes, copperheads, and cottonmouths appear to be more efficient biters with about 75 percent of bites resulting in envenomation. Experiments in laboratories in several parts of the world agree that snakes rarely inject more than half their available venom in a single bite. There is some suggestion that a defensive bite directed against a predator or an animal too large to serve as food results in less venom injection than a bite intended to kill prey. However, rattlesnakes attacking prey may also deliver relatively ineffective strikes (Kardong 1986). The degree to which snakes control the amount of venom injected in various situations remains essentially unknown.

When a rattlesnake or other pit viper delivers an effective bite, pain is usually immediate and intense, although occasionally, and usually with a very severe bite, there may be numbness around the area of the bite lasting as long as 30 minutes. Puncture wounds are obvious and bleed longer and more freely than a nonvenomous wound. Swelling usually begins within a few minutes and spreads both peripherally and centrally. Discoloration around the bite usually is evident within a few minutes. If pain, swelling, and discoloration are absent 15-30 minutes after a pit viper bite, the odds are very good no venom was injected. Important exceptions are individuals bitten by rattlesnakes whose venoms are low in those toxins that are responsible for local swelling and discoloration. This includes some populations of the Mohave rattlesnake, speckled rattlesnake, rock rattlesnake, and tiger rattlesnake. Swelling and discoloration may also be minimal in the rare instance when most of the venom is injected intravenously. However, the individual who sustains such a bite quickly shows signs of generalized poisoning, and the diagnosis of envenomation is rarely in doubt. Individuals under the influence of alcohol or drugs may not have normal pain perception and may display bizarre symptoms. A reliable sign of envenomation, usually seen within the first hour after a bite, is painful swelling of lymph nodes in the groin if the bite is on the foot or leg and in the axilla if on the hand or arm.

Tingling of the face and metallic taste in the mouth are common symptoms of rattlesnake bite. Nausea, vomiting, chills, sweating, and thirst are common symptoms of pit viper bites within the first hour. Hemorrhagic blebs may appear within two hours after a bite or be delayed much longer. These symptoms definitely indicate poisoning but not necessarily a serious or life-threatening bite.

A persistent fall in blood pressure is probably the most reliable indication of a serious pit viper bite. This may manifest itself as faintness or loss of consciousness with pallor and a weak, rapid pulse. Other ominous signs are generalized muscular twitching, widespread appearance of large hives (angioneurotic edema), diarrhea, contracted pupils, and sensation of yellow vision. All may develop within an hour after the individual is bitten.

Coral snake bites are not very painful; there is little or no swelling and no discoloration. Fang punctures bleed little and may be almost undetectable a few hours after the bite. Characteristically there is an asymptomatic period that can last up to seven hours. In fact, in about half the cases, no definite signs of poisoning ever develop. Not many cases of coral snake bites have been reported in detail, but symptoms seem to be quite variable. Sometimes, there are pains radiating from the location of the bite or in the abdomen. Serious manifestations include drooping of the eyelids, difficulty in speaking and swallowing, generalized muscular weakness and incoordination, drowsiness, and difficulty in breathing. This can progress to a complete and fatal paralysis.

A curious and not well understood phenomenon is that of venomous bites by presumably nonvenomous snakes of the family Colubridae. Some colubrids have enlarged, grooved fangs in the rear of the upper jaw, and at least two African species are unequivocally dangerous. A few species with this type venom apparatus just enter the United States along the Mexican border, and a few cases of mild venomous bites by them have been reported. The most serious cases reported in the United States have resulted from bites of Asian snakes such as the yamakagashi (*Rhabdophis tigrinus*) and red-necked keelback (*R. subminiatus*) purchased as innocuous pets (Mittleman & Goris 1974, Cable *et al.* 1984). These snakes have enlarged but ungrooved teeth in the rear of the upper jaw. Poisoning by these snakes results in a dramatic decrease in certain blood clotting factors with resultant internal and external hemorrhages and related complications. *Rhabdophis* is closely related to the North American garter snakes (*Thamnophis*) and water snakes (*Nerodia*), so it is not surprising that a few cases of envenomations characterized by pain, swelling, and ecchymosis have been reported following bites of garter snakes. Two plentiful and widely distributed species, the wandering garter snake (*T. elegans vagrans*) and common garter snake (*T. sirtalis*) have been implicated. Similar cases have been reported following bites by hognose snakes (*Heterodon*). However, perhaps only one in several thousand bites by these presumably nonvenomous colubrids results in poisoning. The answer may be in the nature of the colubrid venom apparatus. Duvernoy's gland, roughly the equivalent of the pit viper venom gland, has a highly toxic secretion in at least some colubrid snakes. But it has a very small lumen for venom storage. And a solid tooth is not so effective for introducing venom into a wound as one that is grooved or hollow. When a colubrid snake feeds, it often holds and chews its prey. This gives time for Duvernoy's gland to secrete venom which is worked into wounds made by the teeth. It probably is significant that a majority of human envenomations by colubrids involve snakes that hung on for several seconds. And in some cases, a captive snake bit when being offered food.

First Aid and Definitive Treatment

Stated simply, the objectives of snakebite treatment are: (1) Remove venom before it can combine with target tissues. (2) Neutralize venom that cannot be removed. (3) Counteract effects of venom that cannot be neutralized. (4) When all the above fail, repair the damage.

Snakebite treatment in the United States has seen a number of colorful and downright dangerous procedures advocated, sometimes by scientists and physicians. In southern Indiana in the 1920's and 30's, whiskey was a popular remedy; nearly every farmer kept a bottle or two "just in case." Other popular treatments were application of the split body of a freshly-killed chicken to the bite or soaking the bitten part in kerosene or turpentine. First aid techniques involving ligature, incision, and suction have been widely advocated and are sound in principle but

of dubious value in practice. Ligatures increase pain and have little effect in retarding spread of venom. Incision followed by suction does facilitate removal of some venom. However, incisions may damage large blood vessels, nerves, or tendons, provide entry for infection, and be followed by serious blood loss particularly since many snake venoms markedly impair blood coagulation. Excision—cutting out the entire area around a bite—is almost certain to do more harm than good and cannot be recommended. Chilling the area around a bite by use of ice or chemical spray with or without a ligature is ineffective and can do serious damage if continued for a prolonged period. Recently, electric shock using high voltage, low amperage current from an outboard motor, lawn mower, or other source has been suggested as first aid for snakebite. The method is under investigation but cannot currently be advocated.

As already mentioned, most persons bitten by snakes can reach definitive medical care within 30-50 minutes. Realizing this, I have maintained for the last decade or so that the most useful snakebite first aid kit consists of car keys and some coins for a call to a hospital. If at all possible, the actual driving to the hospital should be entrusted to someone else. The stress of driving in traffic does not help a snakebite and vice versa. Calling ahead is important. It gives the emergency room time to prepare for the patient's arrival, and the physician on duty can consult with colleagues or call a Poison Information Center if he wishes. The snake should be brought to the hospital with the victim if possible so its identity can be verified. It is better if the reptile is dead. A live snake in a hospital emergency room is a needless distraction and sometimes a hazard. Identification is especially important if a coral snake is suspected, for harmless mimics of coral snakes occur in many parts of the United States. In cases of bites by exotic snakes kept as pets, identification of the reptile is very important also.

Two relatively new procedures seem to be effective and safe enough that their use can be cautiously advocated for the small number of snakebites that occur under circumstances such that a delay of 30 minutes or more in reaching a medical facility can be anticipated. One is the use of elastic bandages such as are widely used to treat sprains wrapped snugly over the area of the bite and extended up the bitten limb to the trunk if there is enough bandage. I am told that panty hose make an acceptable substitute. The limb is then immobilized with a splint. The bandages are left in place until the victim reaches the hospital and preparations for beginning intravenous administration of antivenom have been made. Both experimental and clinical evidence indicate the technique is quite effective in preventing absorption of venom from a bitten limb (Sutherland 1983, pp. 22-32). The method was developed in Australia where the important snakes have venoms that are highly lethal but not very destructive locally. If used for treating bites by rattlesnakes and other pit vipers whose venoms cause significant local damage, it must be with the realization that generalized poisoning may be prevented at the cost of increasing local damage. It is the recommended procedure for bites by coral snakes whose venoms are more like those of Australian snakes.

Another new technique is use of a two-chambered suction device that produces one atmosphere negative pressure. This is applied to the bite as quickly as possible *without* making any incisions and left in place about three minutes. Suction can be repeated as necessary. Preliminary animal experiments indicate up to half an injected dose of rattlesnake venom can be removed. The device was also tested on three persons bitten during a rattlesnake roundup in the Southwest with apparently good results (Bronstein *et al.* 1985). Sawyer Products of Long Beach, California, markets the device in a small, light, durable kit suitable for field use.

Scientific evaluation of these and other first aid measures has been possible through development of very sensitive and specific enzyme-linked immunoassay (ELISA) for snake venoms. Although these tests are not generally available in the United States, enough experimental work has been done to demonstrate their value both in diagnosis of snakebite and evaluation of treatment. Since the test can be done in about two hours, determining presence of venom in blood and urine can be helpful in distinguishing a relatively minor bite from a potentially serious one. These assays have also contributed to better understanding the pathophysiology of snake envenomation. One interesting observation is that venoms of some snakes can be detected at the site of a bite after several days.

Although it is not the purpose of this review to discuss hospital management of snakebite, something should be said about antivenom. This is the only clinically effective antidote for snake venom poisoning and is produced commercially by hyperimmunization of horses with snake venoms. The product commonly used in the United States is made against venoms of three species of rattlesnakes and a large neotropical pit viper of the genus *Bothrops*. It is at least somewhat effective in neutralizing venoms of all North American pit vipers and the most important neotropical species as well as those of a few Old World vipers. A coral snake antivenom is available in limited quantity in those states where coral snakes occur. Antivenoms are by no means ideal therapeutic agents. Their neutralizing capacity is relatively low, hence large doses—400 ml or more—sometimes must be given in a very severe envenomation. Not all venoms and venom fractions are equally well neutralized. Antivenoms have little effect against the factors in pit viper venoms that cause local swelling and necrosis. Being foreign proteins, antivenoms commonly cause serum sickness, less frequently anaphylaxis and other forms of immunologic injury. Significant improvement in antivenoms can be anticipated. Experimental antivenom prepared by affinity chromatography has much better neutralizing capacity and is less likely to cause anaphylaxis (Russell *et al.* 1985). A commercial product could be available in a relatively short time. Monoclonal antibodies have been produced against several snake venom toxins, but their therapeutic use has not been explored.

Except in most unusual situations, antivenom should be given in a hospital. This is but one of numerous reasons why hospitalization is recommended for all but obviously trivial snakebites. Blood pressure and other vital signs are more easily monitored, and hypovolemic shock, the commonest cause of death in pit viper bites, can be detected early and corrected. Other dangerous complications of snakebite such as coagulopathy, renal failure, respiratory failure, and infection can also be detected early and dealt with more effectively. In a series of 9 fatal rattlesnake bites in Arizona, two individuals refused to go to the hospital and three others reached the hospital after delays of 1.5 to 29 hours (Hardy 1986).

A single nonfatal snakebite confers no effective immunity, and evidence of immunity in professional and religious snake handlers who have survived many bites is equivocal. Some have died of snakebite after surviving ten or more previous bites. Immunization with toxoid, a strategy highly successful in infections such as diptheria and tetanus, has been attempted with detoxified snake venoms. The only large scale trial, in the Ryukyu Islands, was not particularly successful (Sawai *et al.* 1969), but the procedure is being considered in some other regions of very high snakebite incidence. In the United States it would be appropriate only for a very small number of individuals. The best single preventative measure is to avoid deliberate contact with venomous snakes. "Illegitimate" snakebites, those sustained by individuals who knowingly place themselves at risk, make up roughly half the snakebites reported in the United States.

Literature Cited

Bronstein, A. C., F. E. Russell, J. B. Sullivan, N. B. Egen, and B. R. Rumack. 1985. Negative pressure suction in field treatment of rattlesnake bite. Vet. Hum. Toxicol. 28:297, 485.

Cable, D., W. McGehee, W. A. Wingert, and F. E. Russell. 1984. Prolonged defibrination after a bite from a 'nonvenomous' snake. JAMA 251:925-926.

Fiero, M. K., M. W. Seifert, T. J. Weaver, and C. A. Bonilla. 1972. Comparative study of juvenile and adult prairie rattlesnake (*Crotalus viridis viridis*) venoms. Toxicon 10:81-82.

Glenn, J. L. and R. C. Straight. 1982. The rattlesnakes and their venom yield and lethal toxicity. *IN* Tu, A. T. (ed.) Rattlesnake Venoms: their Actions and Treatment. New York. Marcel Dekker. Pp. 3—119.

Glenn, J. L., R. C. Straight, M. C. Wolfe, and D. L. Hardy. 1983. Geographical variation in *Crotalus scutulatus* (Mojave rattlesnake) venom properties. Toxicon 21:119-130.

Hardy, D. L. 1986. Fatal rattlesnake envenomation in Arizona. J. Tox. Clin. Tox. 24:1-10.

Kardong, K. V. 1986. The predatory strike of the rattlesnake: when things go amiss. Copeia 1986:816-820.

Minton, S. A. 1953. Variation in venom samples from copperheads and timber rattlesnakes. Copeia 1953:212-215.

———— 1967. Observations on toxicity and antigenic makeup of venoms of juvenile snakes. *IN* Russell, F. E. and P. R. Saunders (eds.) Animal Toxins Oxford. Pergamon Press. Pp. 211-222.

Minton, S. A., and S. A. Weinstein. 1986. Geographic and ontogenic variation in venom of the western diamondback rattlesnake (*Crotalus atrox*). Toxicon 24:71-80.

Mittleman, M. B., and R. C. Goris. 1974. Envenomation from the bite of the Japanese colubrid snake *Rhabdophis tigrinus*. Herpetologica 30:113-119.

Neill, W. T. 1957. Some misconceptions regarding the eastern coral snake, *Micrurus fulvius*. Herpetologica 13:111-118.

Parrish, H. M., and M. S. Khan. 1967. Bites by coral snakes: reports of 11 representative cases. Amer. J. Med. Sci. 253:561-566.

Reid, H. A. 1964. Cobra-bites. Brit. Med. J. 2:540-545.

Reid, H. A., and R. D. G. Theakston. 1978. Changes in coagulation effects by venoms of *Crotalus atrox* as snakes age. Am. J. Trop. Med. Hyg. 27:1053-1057.

Russell, F. E. 1980. Snake Venom Poisoning. Philadelphia. Lippincott.

Russell, F. E., J. B. Sullivan, N. B. Egan, W. S. Jeter, F. S. Markland, W. A. Wingert, and D. Bar-or. 1985. Preparation of a new antivenin by affinity chromatography. Amer. J. Trop. Med. Hyg. 34:141-150.

Sawai, Y., Y. Kawamura, T. Fukuyama, T. Okonogi, and I. Ebisawa. 1969. Studies on the treatment of habu (*Trimeresurus flavoviridis*) bites, VIII. A field trial of prophylactic immunization of habu venom toxoid. Jap. J. Exp. Med. 39:197-212.

Sutherland, S. K. 1983. Australian Animal Toxins. Melbourne. Oxford University Press.

Weinstein, S. A., S. A. Minton, and C. E. Wilde. 1985. The distribution among ophidian venoms of a toxin isolated from the venom of the Mojave rattlesnake (*Crotalus scutulatus scutulatus*). Toxicon 23:825-844.

Honorary Life Members

Ewart M. Baldwin
Irven O. Buss
L. C. Cady
Charles D. Campbell
Robert L. Carr
Julian L. Culbertson
Rexford Daubenmire
Glenn Deitschman
R. A. Diettert
Bruce V. Ettling
William K. Ferrell
C. Clement French
Stanley P. Gessel
N. S. Golding
Phil Haddock
H. P. Hansen
Adolph Hecht
Kenneth Holmes
G. Brooks King
Rufus W. Kiser
Lewis and Clark High School Library (In memory of Thomas Large and J. G. McCracken)
Joseph W. Mills
Milton M. Mosher
Richard J. Naskali
Frank D. Nicol
Frances J. Schadegg
C. Gardner Shaw
Leona M. Sundquist
Oscar Sziklai
Robert F. Tarrant
Richard B. Walker
D. J. Wort

1986 Sustaining Institutional Members

Battelle Northwest, Richland, Washington
EG&G Idaho, Inc., Idaho Falls, Idaho
MacMillan Bloedel, Ltd., Nanaimo, British Columbia, Canada
Potlatch Corporation, Lewiston, Idaho
The Washington Water Power Company, Spokane, Washington
Weyerhaeuser Company, Centralia, Washington

1986 Institutional Members

Boise State University, Boise, Idaho
British Columbia Institute of Technology, Burnaby, British Columbia, Canada
Central Oregon Community College, Bend, Oregon
Central Washington University, Ellensburg, Washington
Centralia College, Centralia, Washington
College of Idaho, Caldwell, Idaho
Eastern Montana College, Billings, Montana
Eastern Oregon State College, LaGrande, Oregon
Eastern Washington University, Cheney, Washington
Edmonds Community College, Lynnwood, Washington
The Evergreen State College, Olympia, Washington
George Fox College, Newberg, Oregon
Grays Harbor College, Aberdeen, Washington
Green River Community College, Auburn, Washington
Highline Community College, Midway, Washington
Idaho State University, Pocatello, Idaho
Lewis-Clark State College, Lewiston, Idaho
Lewis and Clark College, Portland, Oregon
Linfield College, McMinnville, Oregon
Montana College of Mineral Science and Technology, Butte, Montana
Mt. Hood Community College, Gresham, Oregon
North Idaho College, Coeur d'Alene, Idaho
Northern Montana College, Havre, Montana
Pacific Lutheran University, Tacoma, Washington
Pacific University, Forest Grove, Oregon
Peninsula College, Port Angeles, Washington
Portland State University, Portland, Oregon
St. Martin's College, Lacey, Washington
Shoreline Community College, Seattle, Washington
Simon Fraser University, Burnaby, British Columbia, Canada
Skagit Valley College, Mount Vernon, Washington
Southern Oregon State College, Ashland, Oregon
Southwestern Oregon Community College, Coos Bay, Oregon
Spokane Falls Community College, Spokane, Washington
University of Alaska, Fairbanks, Alaska
University of Idaho, Moscow, Idaho
University of Montana, Missoula, Montana
University of Puget Sound, Tacoma, Washington
University of Victoria, British Columbia, Canada
University of Washington, Seattle, Washington
Walla Walla College, College Place, Washington
Washington State Library, Olympia, Washington
Washington State University, Pullman, Washington
Western Washington University, Bellingham, Washington
Whitman College, Walla Walla, Washington
Whitworth College, Spokane, Washington
Yakima Valley College, Yakima, Washington

1986 Sustaining Individual Members

Donald J. Brown, Richland, Washington
Randall E. Brown, Pasco, Washington
Nelsa M. Buckingham, Port Angeles, Washington
John H. Crow, Port Murray, New Jersey
Bruce Ettling, Vancouver, Washington
George R. Fahnestock, Seattle, Washington
William H. Funk, Pullman, Washington
Gerald H. Haddock, Wheaton, Illinois
Donald Hanley, Seattle, Washington
Charles R. Hatch, Moscow, Idaho
Mary M. Hektner, Arcata, California
Francis R. Herman, Fairbanks, Alaska
Richard K. Hermann, Corvallis, Oregon
Barry L. Keller, Pocatello, Idaho
Giles W. Maloof, Boise, Idaho
Emmett B. Moore, Jr., Richland, Washington
Howard R. Panik, Carson City, Nevada
William H. Rickard, Richland, Washington
Edward S. Schreiner, Port Angeles, Washington
Dale Stradling, Cheney, Washington
Robin J. Tausch, Reno, Nevada
Daniel W. Uresk, Rapid City, South Dakota
George H. Ward, Husum, Washington
Shepard M. Zedaker, Christiansburg, Virginia

Northwest Science

General Information

Publication in *Northwest Science* is open to scientists in the basic, applied, and social sciences who are engaged in original or fundamental research. *Northwest Science* does not publish notes, letters, or bibliographic papers. All submissions are reviewed by at least two referees and one associate editor. While submissions from outside the Pacific Northwest are welcome, at least one author of all papers considered for publication must be a member of the Northwest Scientific Association.

Information for Authors—A complete copy of the *Northwest Science* "Information for Authors" is available from the Editor.

Page Charges—Page charges are currently $60 per printed page. Petition for partial payment or waiver of these charges should be directed to the Editor upon the manuscript's being accepted for publication.

Manuscripts—Submit three copies of the paper (including tables and figures) to the Editor. Manuscripts should be typewritten on 8½x11 paper and *double-spaced throughout (including abstract, acknowledgments, literature cited, tables, and legends for figures);* provide ample margins. Avoid unnecessary footnotes. Do not break words at the end of a line. Format and style of manuscripts should conform to general usage in recent issues.

An abstract, written in complete sentences and not exceeding 250 words, should precede every article. It should succinctly state the objectives, the experimental design, the principal observations, and conclusions of the paper. Authors are reminded of the diverse disciplines and readership served by the journal; with this in mind, the abstract should conclude with a sentence or two stating the broader significance of the paper.

Literature citations should have the author's name and year of publication in the text; e.g. (Jones 1978). Citations should be double-spaced and listed in alphabetical order at the end of the article.

Present all data in international (SI) units. English equivalents may be added parenthetically. Use the 24-hour clock (0600 and 2300) and continental dating (17 November 1982).

Equations should be presented camera-ready. Symbols should be large enough to be legible after a ⅓ to ½ reduction in size, but not overly large.

Tables should be typewritten (double-spaced) separately from the text. Original art work or glossy prints of photographs must be submitted for reproduction. Art work and lettering should be large enough (but not overly large) to provide clarity after a 50 percent reduction in size for printing. The author's name and figure number should be penciled on the back of each illustration. Provide a scale for distance on map illustrations. Legends for illustrations should be typed (double-spaced) as a section of the manuscript; do not use a separate page for each legend.

Length of manuscripts is limited to 15 pages of printed copy. Two typed pages are approximately equal to one journal page.

Authors of Biological Papers—On first mention, a species should be designated by common name followed by systematic binomial. For abbreviations and forms of titles for serial publications, follow the *BIOSIS List of Serials.* Consult with the *Council of Biology Editors (CBE) Style Manual,* 4th ed., for general information on manuscript preparation.

Correspondence—Correspondence will be between senior author and the Editor.

Editing—In addition to being reviewed by two referees and an associate editor, manuscripts will be edited for grammatical correctness and clarity.

Galley Proofs and Reprints—One set of proofs will be sent to the senior author for correction shortly before publication; proofs should be returned to the Editor within three days of receipt. Senior authors should inform the Editor of any change of address for handling proofs. Reprints must be ordered when the proofs are returned. A schedule of reprint prices will be sent to the author with the proofs.

Non-Profit Org.
BULK RATE
U.S. POSTAGE
PAID
PULLMAN, WA
Permit No. 1

Northwest Science

Quarterly Publication of the Northwest Scientific Association

MR F N MacMILLAN
WSU/HOLLAND LIBRARY
PULLMAN WA 99164-5610

NWS

Papers published in *Northwest Science* are indexed in *Current Contents, Science Citation Index, Biological Abstracts, The Zoological Record, Recent Literature Supplement to The Auk, Abstracts in Anthropology, Bibliography and Index of Geology, Chemical Abstracts, Bibliography of Agriculture, Forestry Abstracts,* and *University Microfilms.*

Northwest Science is offered in exchange to other colleges, universities, learned societies, and libraries. Publications sent in exchange should be addressed to Washington State University Library, Technical Services Division, Pullman, Washington 99164-5610, U.S.A.

8489

August 1987 Volume 61, Number 3

NORTHWEST SCIENCE

CONTENTS

139 Soil-Vegetation Relationships in a Subalpine Grassland in Northeastern Washington—**Cindy Jo Talbott Roché and Alan J. Busacca**

148 Vesicular-Arbuscular Mycorrhizae of Halophytic Grasses in the Alvord Desert of Oregon—**Iwan Ho**

152 A Method for Assessing Landslide Potential as an Aid in Forest Road Placement—**S. H. Duncan, J. W. Ward and R. J. Anderson**

160 Plant Survival, Growth Form and Regeneration Following the 18 May 1980 Eruption of Mount St. Helens, Washington—**A. B. Adams, V. H. Dale, E. P. Smith and A. R. Kruckeberg**

171 Fall-Winter Habitat Use by Elk in the Shrub-Steppe of Washington—**Scott M. McCorquodale**

174 Seasonal Use of Roost Sites by Merriam's Wild Turkey Hens and Hen-Poult Flocks in Oregon—**R. Scott Lutz and John A. Crawford**

179 Sorted Stone Nets and Circles of the Columbia Plateau: A Hypothesis—**George W. Cox and Douglas W. Allen**

186 Downstream Migration Timing of Two Stocks of Sockeye Salmon on the Mid-Columbia River—**Charles M. Peven**

191 A Comparison of Three Methods for Measuring Arthropod Abundance in Tundra Habitats and its Implications in Avian Ecology—**Christopher J. Norment**

199 Glyphosate Treatment and Deer Mice in Clearcut and Forest—**D. Chris Ritchie, Alton S. Harestad and Ralph Archibald**

Northwest Scientific Association

(Founded 1923)

The Northwest Scientific Association, an affiliate of the American Association for the Advancement of Science, is an association representative of the basic and applied sciences and of social sciences.

Membership in the Northwest Scientific Association, which includes a subscription to *Northwest Science,* is open to individuals in the Northwest (Washington, Idaho, Oregon, Western Montana, British Columbia), for $14 per year ($8 per year for students). Institutional memberships, $40 per year. All other individual subscribers $25 per year. Sustaining membership, $25 per year for individuals and $100 per year for organizations, institutions, or agencies. Subscriptions are for the calendar year only.

Send change of address, payment of dues, or requests for undelivered issues to the Treasurer.

Editor of *Northwest Science*

Kenneth V. Kardong
Department of Zoology
Washington State University
Pullman, Washington 99164-4220

Officers of the Association

President Steven D. Tesch*
Oregon State University
Corvallis, Oregon (1989)

President-Elect W. H. Rickard
Pacific Northwest Laboratory
Richland, Washington (1990)

Secretary George H. Fahnestock
Seattle, Washington (1990)

Treasurer Robert K. Moseley
The Nature Conservancy
1221 South Main Street
Moscow, Idaho 83843 (1989)

Past President Donald Hanley
Washington State University
c/o University of Washington
Seattle, Washington (1988)

Trustees:

Robert Antibus
University of Montana
Missoula, Montana (1988)

Steven Benham
Pacific Lutheran University
Tacoma, Washington (1988)

Dan L. Campbell
United States Dept. of Agriculture
Olympia, Washington (1990)

Robert L. Carr
Eastern Washington University
Cheney, Washington (1990)

Richard A. Cellarius
Evergreen State College
Olympia, Washington (1988)

Wilbert R. Danner
University of British Columbia
Vancouver, B.C. (1989)

Kenneth Hammond
Central Washington University
Ellensburg, Washington (1989)

David Hansen
Pacific Lutheran University
Tacoma, Washington (1990)

Larry Larson
Oregon State University
Corvallis, Oregon (1988)

William Lopushinsky
U.S. Forest Service
Wenatchee, Washington (1990)

Gilbert B. Pauley
University of Washington
Seattle, Washington (1989)

William R. Rayburn
Washington State University
Pullman, Washington (1989)

W. H. Rickard
Pacific Northwest Laboratory
Richland, Washington (1988)

Harry Smith
University of British Columbia
Vancouver, B.C. (1988)

Steven D. Tesch
Oregon State University
Corvallis, Oregon (1988)

David H. Wagner
University of Oregon
Eugene, Oregon (1989)

H. Clare Wiser
Washington State University
Pullman, Washington (1990)

*Term of office expires in the year given in parentheses.

August 1987 Volume 61, Number 3

NORTHWEST SCIENCE

Editor	Kenneth V. Kardong	Washington State University
Managing Editor	Fred Bohm	Washington State University
Indexer	Caroline Hooper	
Associate Editors		
Aquatic Biology	Gary L. Larson	U.S. National Park Service/ Oregon State University
Botany	Suzanne M. Schwab	Eastern Washington University
Chemistry and Physics	Frank L. Curzon	University of British Columbia
Engineering and Mathematics	Gary L. Sheldon	Washington State University
Forestry	James K. Agee	U.S. National Park Service/ University of Washington
Geology	Franklin F. Foit, Jr.	Washington State University
Social Sciences	Philip D. Young	University of Oregon
Soils	Robert L. Edmonds	University of Washington
Wildlife Biology	Margaret A. O'Connell	Washington State University
Zoology	Kerry Paul Reese	University of Idaho

CONTENTS

139 Soil-Vegetation Relationships in a Subalpine Grassland in Northeastern Washington—**Cindy Jo Talbott Roché and Alan J. Busacca**

148 Vesicular-Arbuscular Mycorrhizae of Halophytic Grasses in the Alvord Desert of Oregon—**Iwan Ho**

152 A Method for Assessing Landslide Potential as an Aid in Forest Road Placement—**S. H. Duncan, J. W. Ward and R. J. Anderson**

160 Plant Survival, Growth Form and Regeneration Following the 18 May 1980 Eruption of Mount St. Helens, Washington—**A. B. Adams, V. H. Dale, E. P. Smith and A. R. Kruckeberg**

171 Fall-Winter Habitat Use by Elk in the Shrub-Steppe of Washington—**Scott M. McCorquodale**

174 Seasonal Use of Roost Sites by Merriam's Wild Turkey Hens and Hen-Poult Flocks in Oregon—**R. Scott Lutz and John A. Crawford**

179 Sorted Stone Nets and Circles of the Columbia Plateau: A Hypothesis—**George W. Cox and Douglas W. Allen**

186 Downstream Migration Timing of Two Stocks of Sockeye Salmon on the Mid-Columbia River—**Charles M. Peven**

191 A Comparison of Three Methods for Measuring Arthropod Abundance in Tundra Habitats and its Implications in Avian Ecology—**Christopher J. Norment**

199 Glyphosate Treatment and Deer Mice in Clearcut and Forest—**D. Chris Ritchie, Alton S. Harestad and Ralph Archibald**

Announcements

Research Grants Awarded by the Northwest Scientific Association

Research grants in the amount of $300 were awarded at the annual spring meeting of the Association to each of the following students:

Jennifer A. Clarke, Dept. Zoology, Washington State University
Title: "Folivory strategies for White-Tailed Ptarmigan."

Ruth E. B. Kirkpatrick, Dept. Botany, Washington State University
Title: "An analysis of the mating system of homosporous fern, *Gymnocarpium dryopteris* ssp. *disjunctum*."

Peter V. Lindeman, Dept. Biological Sciences, University of Idaho
Title: "Painted turtle life history in the Pacific Northwest: A comparative study of two contrasting habitats."

Jeffry A. Peterson, Dept. Zoology, Oregon State University
Title: "An investigation of the palatability of *Bufo boreas* and *Rana cascadae* larvae to aquatic insect predators."

Paul G. Wolf, Dept. Botany, Washington State University
Title: "Autopolyploid evolution in *Heuchera grossulariifolia* (Saxifragaceae)."

Research grants to students will be offered again in 1988. More details will appear in the November issue of *Northwest Science.*

Cindy Jo Talbott Roché, Department of Forestry and Range Management
Washington State University, Pullman, WA 99164-6410

and

Alan J. Busacca, Department of Agronomy and Soils
Washington State University, Pullman, WA 99164-6420

Soil-Vegetation Relationships in a Subalpine Grassland in Northeastern Washington[1]

Abstract

Clumps of mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) and subalpine fir (*Abies lasiocarpa*) a few meters in diameter dot the subalpine grassland on Calispell Peak in northeastern Washington. The pattern of vegetation is associated with soil properties, primarily rock content, with snow depths, and with exposure to wind and sun. The grassland occurs on soils that are shallow and stony. Clumps of subalpine fir within the grassland occur on pockets of soil that are deeper and less stony. Clumps of mountain big sagebrush and bluebunch wheatgrass (*Agropyron spicatum*) occur on microtopographic mounds of soil that also are deeper and less stony. Because of the differences in rock content, soils of the grassland have only about 60 percent as much available water holding capacity as do those of the mound and tree island. The snowpack, measured on the windward grassland, was thin and contained only 10 to 60 percent as much water per unit area as the deeper snowpack on the leeward slope and under forest canopy. A buried layer of Mount St. Helens "T" volcanic ash indicated that since 1800 AD 5 cm of soil material has accumulated on the mound site and 10 cm under the subalpine fir by vegetation trapping airborne dust. Bands of charcoal within the mound record one fire in the grassland about 1500 AD, and two fires since 1800 AD. Grass balds in areas of otherwise continuous forest cover are often local landmarks. Conditions that lead to these timberlines are of interest to the general public as well as professionals. The reasons why trees have not replaced the grassland may tell about the recent history of the region or have implications for management of these areas.

Introduction

Grassland communities occur on south- and west-facing ridges of some of the highest peaks in northeastern Washington and northern Idaho. The existence of these "grass balds" has long sparked the interest of ecologists (Shaw 1909, Daubenmire 1944). Daubenmire (1968) attributed these subalpine parks in northern Idaho and northeastern Washington to failure of tree seedlings to survive late summer drought. Daubenmire (1981) hypothesized that localized droughty conditions prevail on exposed ridges because wind transfers snow from windward slopes onto protected leeward slopes. Exposure of the south- and west-facing slopes to desiccating winds and direct solar radiation increases evapotranspiration and intensifies the droughty conditions.

During a reconnaissance of vegetation on one such grass bald on Calispell Peak, scattered clumps of subalpine fir (*Abies lasiocarpa*)[2] were observed in the grassland above the elevation of continuous forest cover. We hypothesized that differences in soil properties or microtopography within the grass bald might have had localized effects on plant growth and therefore have played a role in the distinctive vegetation patterns. We described the vegetation and microtopography of a representative part of the grassland and described and sampled soils to test our hypothesis. Secondarily, we have been able to interpret aspects of the history of the grass bald from features found in the soil profiles and from the properties of the soils.

Study Area

Calispell Peak has an elevation of 2072 m (6837 ft) and is located at 48° 26' 13" N. and 117° 30' 04" W. Approximately 200 hectares of grassland dominate the southeast to west exposures from 1760 to 2060 m (5800 to 6800 ft) elevation (Figure 1).

The principal soil series mapped on Calispell Peak is Brickel stony loam (Donaldson *et al.* 1982). Soils of Brickel series are classified as loamy-skeletal, mixed Typic Cryoborolls. The Brickel series consists of moderately deep, well-drained soils that have formed in residuum,

[1]Scientific Paper No. 7426. Contribution from the College of Agriculture and Home Economics Research Center, Washington State University. Projects 2211 and 0900.

[2]Taxonomy according to Hitchcock and Cronquist (1973), except for *Artemisia* which is described by Beetle (1960).

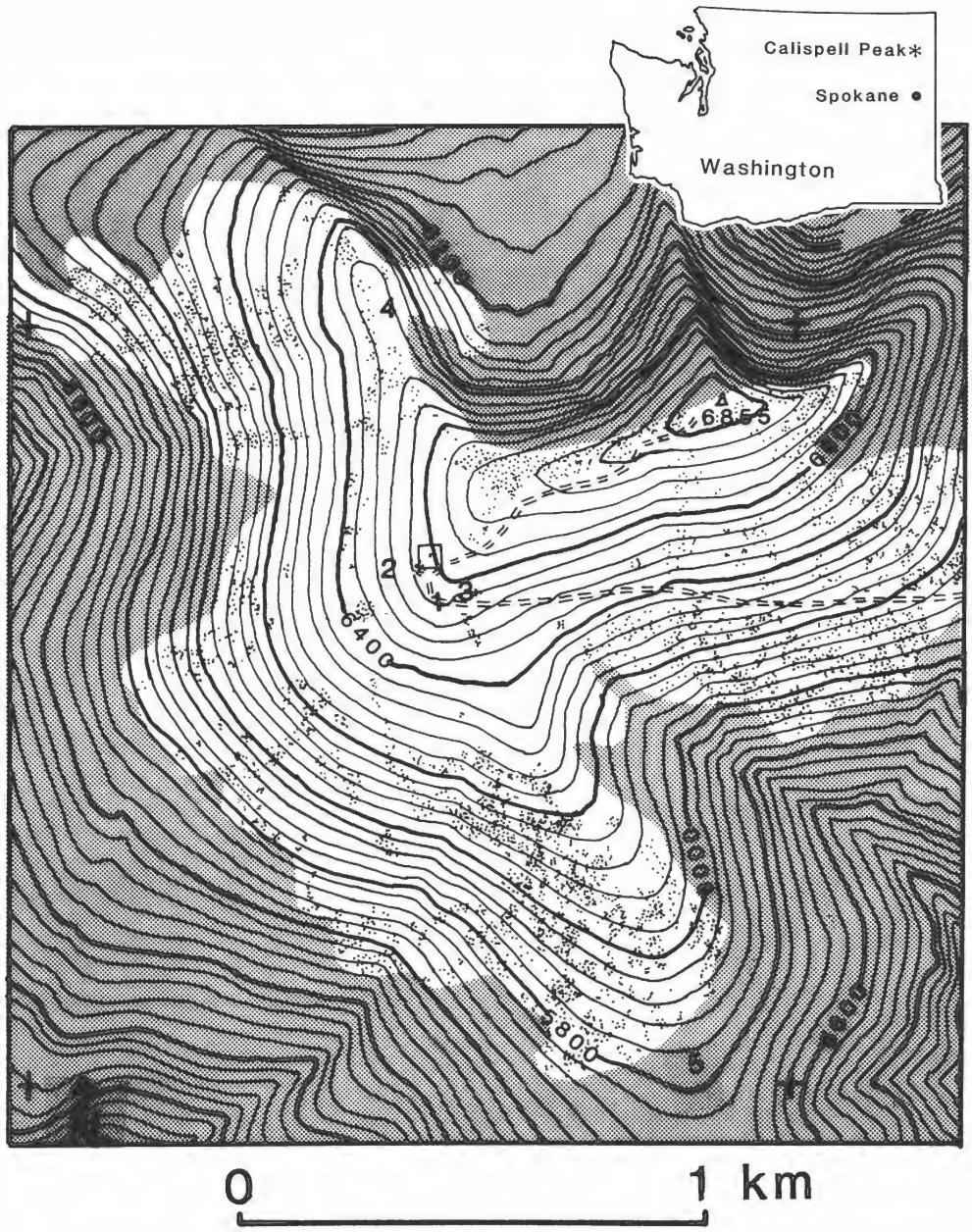

Figure 1. Location and topography of Calispell Peak in northeastern Washington. Shaded area is forested, individual dots show location of tree islands and white is grassland area. Open box shows soils pedon sampling area. Numbers correspond to snow survey sites discussed in text. Contour interval is 40 feet, elevations are in feet. Adapted from U.S.G.S. Calispell Peak Quadrangle, 7.5 minute series.

colluvium, and glacial till from granitic rock mantled with an admixture of volcanic ash and loess.

Since the upper limit of glacial deposits mapped for the latest Pleistocene glaciation is 1524 m (5000 ft) in the vicinity of Calispell Peak (Flint 1937), the upper part of the mountain was likely ice-free. The land surface before addition of volcanic ash and loess in post-glacial time was not glacial till but residuum from granite and gneiss.

Methods

The vegetation has been classed into three community types based on the dominant cover of grass, shrubs or trees. We refer to these as intermound (grass), mound (sagebrush) and tree island, respectively.

After reconnaissance of the grass bald on foot and after observing patterns of soil depth, rock content and vegetation in a roadcut exposure for a distance of approximately one kilometer, we selected a representative site for our sampling. The site has areas of intermound, mound and tree island within a 10 m radius. This site is about two-thirds of the way up the windward, grassed part of the peak (Figure 1).

One soil pedon for each of the three vegetative types was described and sampled on 20 August 1984. We determined particle size distribution and soil water release curves for the fine earth fraction (<2 mm) of each horizon sample by standard methods (Soil Conservation Service 1982). The pressure-plate extraction method for soil water release was modified by wetting the soil samples before placing them on the plate because the soils were hydrophobic and did not wet readily by the standard procedure. Total soil carbon of horizon samples was analyzed by dry combustion using a LECO furnace model CHN 600. We used the soil water release curves and estimates of rock content to calculate total available water storage to 60 cm in each of the three soils.

We sampled and analyzed a layer of volcanic tephra (airborne volcanic material) from the subsurface in the soils of the mound and tree-island (Figure 2) in order to determine the origin and age of the tephra. The volcanic glass in the sample was concentrated by wet sieving and treated with hydrogen peroxide to remove organic matter. Major elements in glass shards of the coarse-silt fraction (20-50 μm) were determined using a Cameca Camebax electron microprobe. We analyzed 20 shards and averaged the results. These analyses were calibrated to an obsidian standard (U of A 5831, Smith *et al.* 1977).

We measured snow depth and water content of the accumulated snow pack on 7 March 1984

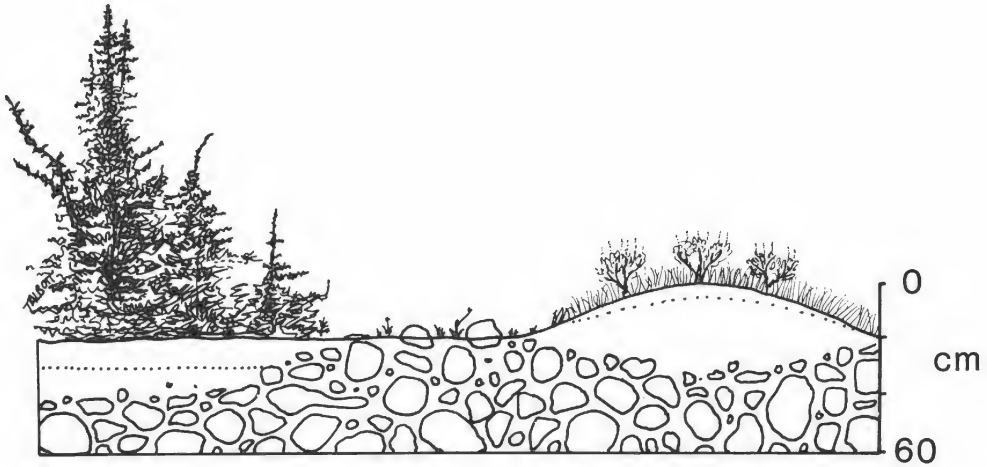

Figure 2. Schematic vertical section showing relationship in position and rock content of the three vegetation types. From left: tree island, intermound, mound. Dotted line is the buried tephra layer.

using standard Soil Conservation Service snow survey procedures (Soil Conservation Service 1973). Measurements were made on the exposed west- and southwest-facing slopes, on the ridgelines, in the lee of each ridgeline and below timberline under the forest canopy (Figure 1).

Results and Discussion

Vegetation

The intermound or grassland area is dominated by a mixture of Idaho fescue (*Festuca idahoensis*) and green fescue (*F. viridula*), with Ivesia (*Ivesia tweedyi*), yarrow (*Achillea millefolium*), western hawkweed (*Hieracium albertinum*), silky lupine (*Lupinus sericeus*), Rocky Mountain aster (*Aster stenomeres*), and subalpine daisy (*Erigeron peregrinus*). Parry's rush (*Juncus parryi*) and tufted hairgrass (*Deschampsia caespitosa*) occur in more moist locations, primarily along roadsides and near late-melting snowdrifts.

Mounds within the grassland support mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*). Rhizomatous bluebunch wheatgrass (*Agropyron spicatum*) forms the dominant understory of the sagebrush mounds.

Tree islands within the grassland are less than about 6 m in diameter and are composed of subalpine fir up to 4.5 m in height. The trees do not appear to be reproducing vegetatively by adventitious rooting of lower branches, but have multiple tops due to repeated damage. Some of the tree islands are doughnut or horseshoe shaped, indicated that the clump may have started as an individual tree that died after other trees became established around it. The understory vegetation of the tree islands includes elderberry (*Sambucus racemosa* var. *melanocarpa*), yarrow, mountain heliotrope (*Valeriana sitchensis*), woodrush (*Luzula hitchcockii*), and sedge (*Carex paysonis*).

Trees on the broad ridge that extends north from Calispell Peak (Figure 1) fit the pattern of "ridgetop ribbon forests" described by Arno and Hammerly (1984) on mountain ridges southwest of Missoula, Montana. A portion of the leeward slope supports no trees because a very deep snow bank lingers late into the growing season, and there exists instead a meadow of sedge (*Carex* spp.) and tufted hairgrass.

Microtopography and Soil Properties

The (sagebrush) mounds comprise only about five percent of the grassland area and so the microtopography cannot be described as classical mound-and-swale, instead it might be described as consisting of infrequent mounds on a sloping hillside. The mounds are several meters in diameter and up to one-half meter higher than the surrounding intermound.

Tree islands also occupy about five percent of the grassland. The land surface is nearly level from the intermound areas to the tree islands, or is slightly concave under the trees (Figure 2).

All of the fine earth (<2 mm) fractions of horizon samples are loamy fine sand, loamy very fine sand, or fine sandy loam (Table 1). Changes in soil texture down each profile appear to result from stratification of parent materials. Rock content of the upper part of the profile is quite different from one soil to another: 5-15 percent in the mound, 50-60 percent in the intermound, and 10-40 percent in the tree island (Table 1; Figure 3). Rock content increases with depth to about 70 percent in the lower part of all three profiles.

The calculated water storage capacity to a depth of 60 cm is 9 cm in the tree island site, 8 cm in the mound site, and only 5 cm in the intermound site (Table 2). The differences in water storage among the sites are largely due to the differences in rock content.

The total carbon content of all three soils decreases with depth (Table 1). The mound soil has the highest carbon content (9.7 to 5.9 percent), followed by the tree-island soil (8.5 to 4.2 percent), and the intermound soil (7.6 to 2.4 percent). Carbon is highest in the surface horizon of the mound soil and decreases gradually with depth, a typical pattern for a grassland soil. The carbon distribution in the soil of the tree island reflects the incorporation of tree litter principally at the surface, and because of this it decreases sharply with depth. The lower overall carbon content in the soil of the intermound reflects the sparser vegetation and the greater proportion of forbs than occur on the other two sites. Few roots penetrate below 50 cm in the intermound soil and this is reflected in a low carbon content below 60 cm (Table 1).

The pattern of vegetation types appears to be strongly associated with the microtopography and with rock content in the soil profiles (Figures

TABLE 1. Soil Properties

Soil Depth (cm)	Total Carbon %	Rock Content (Coarse Fragments) (volume % ≥2mm)	Sand 2.0-0.05 mm	Silt 0.05-0.002 mm (weight %)	Clay <0.002 mm
MOUND					
0-5	9.7	5	75.3	22.8	1.9
5-31	7.1	15	78.8	18.0	3.2
31-36	5.9	40	75.4	21.2	3.4
36-40	—	70	—	—	—
INTERMOUND					
0-8	7.6	50	77.6	18.4	4.0
8-40	5.9	60	63.9	32.4	3.7
40-60	—	70	—	—	—
60-70	2.4	70			
TREE ISLAND					
0-6	8.5	10	74.2	22.3	3.5
6-20	7.0	40	74.4	22.8	2.8
20-54	4.3	50	69.2	29.6	1.2
54-60	4.2	60	74.9	22.2	3.0

TABLE 2. Estimated Water Storage Capacity

Soil Depth (cm)	Available Water[1] (Fine earth[3]) (cm cm^{-1})	Rock Content (Coarse fragments[2]) (volume %)	Available Water Storage per Horizon (Whole soil[2]) (cm)	Total Available Water Storage in Profile[2] (Whole Soil[3]) (cm)
MOUND				
0-5	0.22	5	1.5	
5-31	0.14	15	4.3	
31-36	0.17	40	0.7	
36-60	0.17	70	1.7	
				8
INTERMOUND				
0-8	0.15	50	0.8	
8-25	0.17	60	1.6	
25-40	0.17	60	1.4	
40-60	0.17	70	1.4	
				5
TREE ISLAND				
0-6	0.34	10	2.5	
6-20	0.17	40	2.0	
20-54	0.16	50	3.8	
54-60	0.16	60	0.5	
				9

[1]Available water is the water held between potentials of −0.03 MPa and −1.5 MPa, estimates of field capacity and permanent wilting point.

[2]Total available water storage in the profile is calculated from the available water and the following other factors: A bulk density value of 1.4 Mg m^{-3} is used for all horizons. Estimated storage capacity = cm of soil x available water per cm depth x percent volume of fine earth x bulk density. Water storage is estimated to a uniform depth of 60 cm for all soils. Some plants may draw water from greater depths.

[3]Fine earth consists of mineral particles <2 mm in diameter; coarse fragments are those mineral or rock particles ≥2 mm in diameter; whole soil consists of fine earth plus coarse fragments.

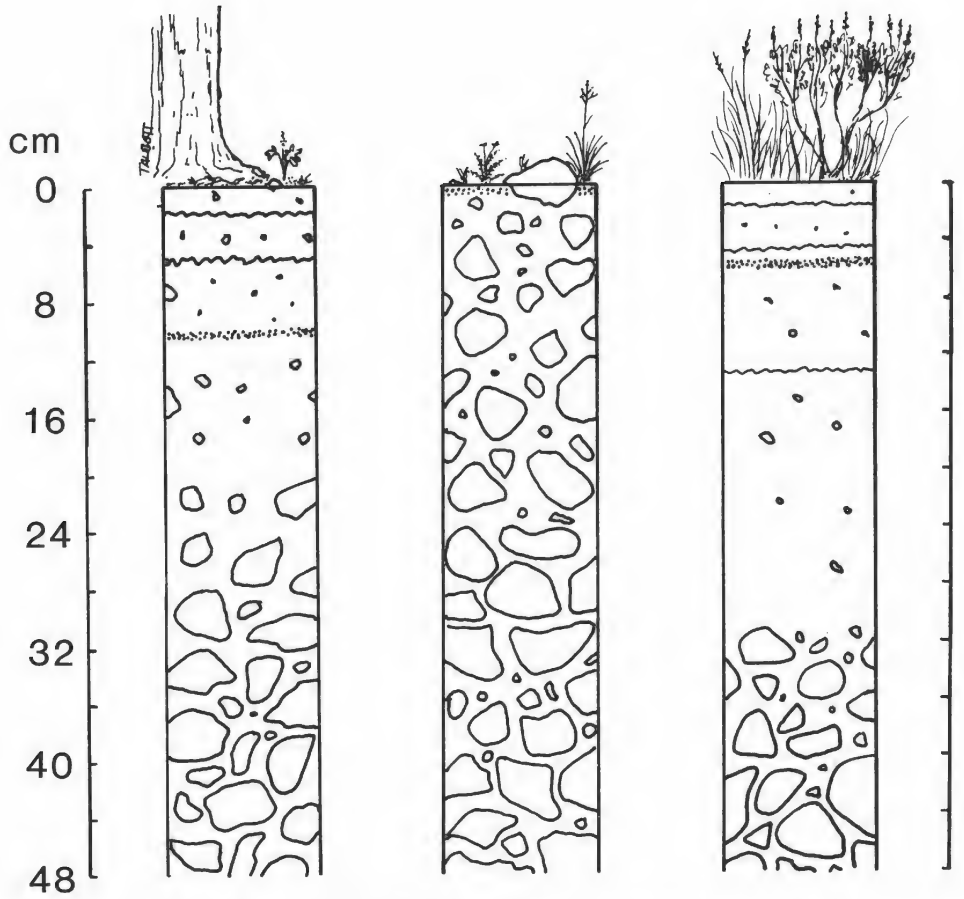

Figure 3. Soil profiles, from left: tree island, intermound, mound. Wavy lines are charcoal layers; dotted lines are volcanic tephra. Soils are not shown in their natural microtopographic relationship to one another.

2, 3). Both of these factors may influence water availability for plant growth: the differences in rock content mean that soils of the sagebrush mound and tree island have almost twice as much available water storage capacity as do soils of the intermound (Table 2). Additionally, drainage of soil water into the stone-free pockets of the tree island may increase the amount of water received. Together, these two factors may lengthen the time during the growing season that water is available for plants in the tree island site.

Tephra and Charcoal in the Soils

Layers of charcoal were found at depths of 2, 4, and 13 cm in the mound soil and at depths of 2 and 5 cm in the tree island soil (Figure 3). We found no charcoal in the intermound soil.

We found two discrete bands of grayish-white volcanic tephra in the soil profiles (Figure 3). The first was within the litter at the soil surface of the intermound site and was from the 18 May 1980 eruption of Mount St. Helens. Silt-sized glass shards dominated the second band of tephra, which was about 1 cm thick and was

preserved at 10 cm depth in the soil profile of the tree island and at 5 cm depth in the soil of the mound. This layer was not preserved in the intermound soil.

The buried tephra in the soils most likely correlates with either the T or W layers from eruptions of Mount St. Helens about 1800 AD and 1480 AD, respectively (Smith *et al.* 1977, Yamaguchi 1983). Both layers have been reported within a few tens of kilometers of Calispell Peak (Smith *et al.* 1977, Okazaki *et al.* 1972).

From electron microprobe analyses of glass shards we calculated the ratio of Ca to Fe to K. This method has been used successfully to identify the origin of tephra layers (Westgate *et al.* 1970, Smith *et al.* 1975). Based on the similarity of this key element ratio in the buried tephra to those reported previously for layer T (Figure 4) we correlate this sample with Mount St. Helens layer T.

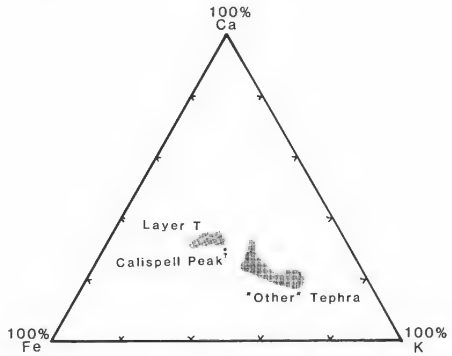

Figure 4. Electron microprobe data for Ca, K, and Fe in glass shards from buried tephra layer on Calispell Peak, Mount St. Helens pyroclastic layer "T," and "other" tephra. Adapted by permission from Smith *et al.* (1975). "Other" tephra include Glacier Peak (upper and lower), Mount Mazama, Mount St. Helens W and Y, Bridge River (three types) and a tephra of unknown origin that is common north of Wenatchee, both east and west of the Okanogan River.

The stratigraphic relationship of layer T to the charcoal layers and a difference in the type of charcoal found in the tree island versus the sagebrush mound provides information about the history of the grassland. The two charcoal bands above the tephra layer represent two fires in the last 186 years. This frequency is consistent with the 90 to 130 year fire recurrence interval in the subalpine fir forests that surround grass balds in the northern Rocky Mountains (Arno 1980). The third band of charcoal, 8 cm beneath the tephra layer in the mound site, records at least one fire before 1800 AD.

The charcoal in the three layers in the sagebrush mound consists of fine filaments, whereas that in the two layers in the tree island consists of pieces of charred wood up to 2 cm long. The fine filaments of charcoal represent burned grasses and forbs indicating that the subalpine grassland has persisted for at least several hundred years on Calispell Peak. The fragments of burned wood in the tree site are evidence that the tree islands also have been a component of the grassland in the pre-historic past. Fragments of burned wood under the tree island and fragments of burned grasses under the mound also indicate to us that fires did not change the dominant vegetation on either the tree or mound sites. Fire could have played a role in maintaining the pattern of vegetation by killing tree seedlings in the grassland or on the outer edges of the tree islands.

Trees are limited to apparent depressions in the original stony bedrock surface. From the low rock content in the A and B horizons of the soils of the tree island and mound and from the dominance of very fine sand in the fine earth we infer that these soils have formed by vegetation trapping airborne dust.

Relatively stone-free mounds also have been observed in subalpine grassland by Daubenmire (1981) on Gisborne Ridge, Bald Mountain (both in Idaho) and Roundtop (in Washington). These mounds, and as well those observed by one of us (Roché) on North and South Baldy Mountains in Pend Oreille County, Washington, are covered by a dense stand of rhizomatous bluebunch wheatgrass and lack sagebrush. Daubenmire (1981) hypothesized that the mounds are solifluction lobes that originated in late-glacial time. The mounds on Calispell Peak appear to have originated by clumps of dense grass or grass-sagebrush cover trapping dust. The presence of tephra layer T indicates that these microtopographic features are much younger than late glacial; the lack of stones and the horizontal bedding of the tephra and charcoal indicate an eolian origin and suggest a lack of solifluction processes in forming the microtopography.

Since the year 1800, windblown soil material has accumulated on the tree site at a net average rate (deposition minus erosion) of 0.5 mm per year and on the mound site at 0.3 mm per year. The absence of either a discrete tephra layer or charcoal bands in the soil of the intermound site indicates net erosion or severe soil mixing on this vegetation type since at least the year 1800.

Pattern of Snow Depth

The minimum thickness of snow, 16.5 cm, which contained 3.8 cm of water, occurred on the break of the north-south ridgeline (site 1, Figure 1). On the windward slope in the grassland, the snow averaged 71 cm in thickness and contained 23.4 cm of water (site 2). A few meters on the lee side of the north-south ridgeline, snow was 114 cm thick and contained 38.7 cm of water (site 3). On the top of the ridge and on its lee side, the snow was deeper than 229 cm (site 4), the maximum length of the snow-measuring equipment. Under continuous forest cover at approximately 1750 m on the windward slope (site 5), the snow averaged 125 cm deep and contained 39 cm of water.

This pattern corresponds to exposure to prevailing southwesterly winds. Wind transfers snow from the grassland on the windward slope and deposits it on the lee side of the ridge where it accumulates to form a thick cornice. As a result, the grassland receives only 10 to 60 percent as much water per unit area from snow as do the forested sites, as measured near the end of the period of snow accumulation. Rates of sublimation may also be higher in the grassland than in forest due to exposure of the snowpack to wind and solar radiation. Measured snow depths are adequate to saturate the soil profiles beneath. However, due to sublimation and early melting of the snow in the exposed grassland, the shallow soils on the southwest slope are likely to retain only a part of this moisture until temperatures become favorable for plant growth. Our snow survey supports Daubenmire's hypothesis (1981) that droughtiness in subalpine grasslands of the area are caused at least in part by wind transfer of snow.

Conclusions

The subalpine grassland on the windward slope of Calispell Peak occurs on shallow stony soils. Wind transfer of snow and low water storage capacity reduce the available soil moisture. High sublimation rates of the snowpack and high evapotranspiration rates due to southwest exposure also may contribute to droughtiness. Trees occur in microsites where the soils are less stony (greater water storage capacity) and in areas where snow accumulates.

The mounds, which have a water storage capacity similar to that of the tree islands, support sagebrush. A key difference between the two microsites could be that the concave-shaped tree sites (Figure 2) receive additional water as runon and throughflow, whereas the convex-shaped sagebrush mounds give up water to runoff and throughflow.

The deeper, less stony soils of the tree islands and mounds have formed by trapping of airborne dust. Using the Mount St. Helens T layer as a dateline, 5 cm of soil material has accumulated on the mound site since the year 1800, and 10 cm has accumulated on the tree island site.

Bands of charcoal in the soil of the mound site record one fire before and two after 1800 AD. These fires may have killed tree seedlings in the grassland, thus preventing expansion of the tree islands. Fire has not prevented establishment of trees, however, where moisture conditions are more favorable: pockets of deeper soil, the ridgetop, and northeast slopes. Using the average net deposition rate of 0.5 mm per year that we calculated for the mound site and assuming a similar rate of soil accumulation before 1800 AD, the band of filamentous charcoal below layer T records a fire in grassland about 1500 AD and provides a minimum age for the subalpine grass bald on Calispell Peak.

Acknowledgments

Larry Laing, former Colville National Forest Soil Scientist, assisted in field work and profile descriptions. Ann and Gilbert Peavey provided snowmobiles and assisted with snow measurements. Monica Engle provided guidance in the particle-size determinations. Kees Calissendorff worked with us in the measurement of soil water release curves. R. Alan Black reviewed the manuscript. Thanks also are due to Ben Roché for discussion and review of the manuscript and for providing a truck for field work.

Literature Cited

Arno, S. F. 1980. Forest fire history in the northern Rockies. J. For. 78:460-465.

Arno, S. F., and R. P. Hammerly. 1984. Timberline: Mountain and Arctic Forest Frontiers. The Mountaineers, Seattle.

Beetle, A. A. 1960. A Study of Sagebrush. Agr. Exp. Sta. Bull. 368. University of Wyoming, Laramie.

Daubenmire. R. F. 1944. Mountain parks in northern Idaho. Ida. Forest. 26:16.

_____. 1968. Soil moisture in relation to vegetation distribution in the mountains of northern Idaho. Ecology 49:431-438.

_____. 1981. Subalpine parks associated with snow transfer in the mountains of northern Idaho and eastern Washington. Northw. Sci. 55:124-135.

Donaldson, N. C., J. T. DeFrancesco, and D. W. Barron. 1982. Soil Survey of Stevens County. USDA-Soil Conservation Service, Washington, D.C.

Flint, R. F. 1937. Pleistocene drift border in eastern Washington. Geol. Soc. Amer. Bull. 48:203-232.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle.

Okazaki, R., H. W. Smith, R. A. Gilkeson, and J. Franklin. 1972. Correlation of West Blacktail Ash with pyroclastic layer T from the 1800 A.D. eruption of Mount St. Helens. Northw. Sci. 46:77-89.

Received 2 December 1986
Accepted for publication 6 February 1987

Shaw, C. H. 1909. The causes of timberline on mountains: the role of snow. Plant World 12:169-181.

Smith, H. W., R. Okazaki, and C. R. Knowles. 1975. Electron microprobe analysis as a test of the correlation of West Blacktail ash with Mount St. Helens pyroclastic layer T. Northw. Sci. 49:209-215.

_____. 1977. Electron microprobe analysis of glass shards from tephra assigned to Set W, Mount St. Helens, Washington. Quat. Res. 7:207-217.

Soil Conservation Service, USDA. 1973. Snow survey sampling guide. Agr. Handbook No. 169, Washington, D.C.

_____. 1982. Procedures for collecting soil samples and methods of analysis for soil survey. Soil Surv. Invest. Rep. No. 1, Washington, D.C.

Westgate, J. A., D. G. W. Smith, and M. Tomlinson. 1970. Late Quaternary tephra layers in southwestern Canada. Proc. 2nd Annual Paleo-environmental Workshop of the University of Calgary Archeological Association. The Student's Press. Calgary, Alberta, Canada. Pp. 13-34.

Yamaguchi, D. K. 1983. New tree-ring dates for recent eruptions of Mount St. Helens. Quat. Res. 20:246-250.

Iwan Ho, U.S. Department of Agriculture, Forest Service
Pacific Northwest Research Station, Forestry Sciences Laboratory
3200 Jefferson Way, Corvallis, Oregon 97331

Vesicular-Arbuscular Mycorrhizae of Halophytic Grasses in the Alvord Desert of Oregon

Abstract

In an eastern Oregon high desert, Alvord Desert (an alkali, dry lake bed), vesicular-arbuscual (VA) mycorrhizal fungi were found in the roots of two halophytic grasses—(*Festuca idahoensis* and *Distichilis stricta*). Four samples were taken from depths of 10, 20, 30, and 40 cm at sixteen randomly selected sampling sites. Abundant spores were found in these generally harsh vegetative environments. Eighty percent of VA-mycorrhizal fungus were *Glomus mosseae,* and the remainder were *G. macrocarpum.* Soil pH ranged from 9.2 to 10.5. Spore numbers were inversely proportional to the concentration of sodium in the soil. Use of VA-mycorrhizal fungi to increase the salt tolerance of plants on vast alkali wastelands could aid in developing rangeland with halophytic grasses and eventually in the reclamation of much of the high-saline soil for crop production.

Introduction

Vesicular-arbuscular mycorrhizal fungi occur with roots of most plant species in nearly all types of habitats, even desolate ones. The alkali Alvord Desert of southeastern Oregon has only 186 mm of rainfall per year, but a preliminary examination of grass roots from the desert revealed heavy mycorrhizal infection. The discovery means that these VA-mycorrhizal fungi might be used to increase salt tolerance of plants on vast alkali wastelands. This could aid in development of new rangeland with halophytic grasses and, eventually, in the reclamation of much of the world's high-saline soil into crop production at the least cost. This paper reports the results of quantitative assessment of VA-mycorrhizae and identification of the fungi.

The Study Area

The Alvord Desert (13 km wide by 18 km long and at an elevation of 1220 m) is a playa in Harney County, southeastern Oregon. Directly to the west of the desert, the Steens Mountains rise abruptly to an elevation of 2950 m. Plateaus and ridges around the other sides of the desert are at elevations of about 1500 m (Figures 1, 2). Water from snow melting in the mountains in spring and from occasional thunder showers in the summer provides moisture for early season growth of many halophytes, including the facultatively halophytic grasses, *Festuca idahoensis* and *Distichlis stricta.*

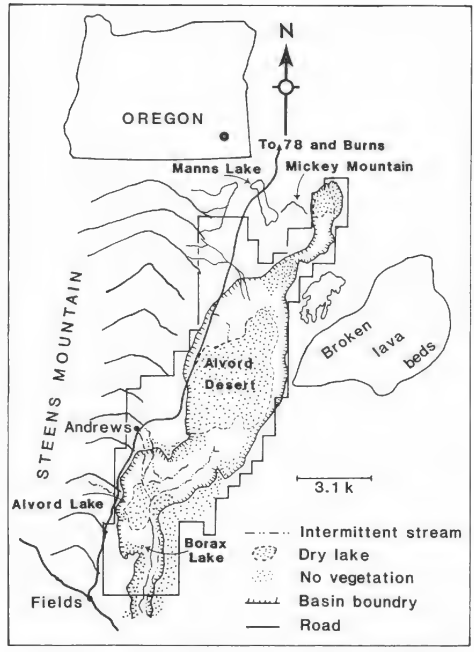

Figure 1. Alvord Desert, southeastern Oregon.

Methods

Sixteen soil and root samples were taken at intervals of about 200 m around the edge of a dry alkaline lake bed 500 m south of the road in the Alvord Desert in July 1979. A 10-cm² hole was dug with a straight-edged shovel at each sample

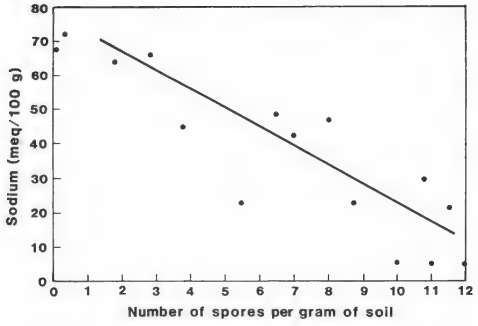

Figure 2. Correlation coefficient of soil sodium concentration vs. spore number.

site. Soil and roots from each hole were segregated by 10-cm depth classes down to 40 cm. A separate, adjacent sample was taken for soil analysis at a depth of 20 cm. Species composition of the surface vegetation was recorded at the same time.

Soil and root samples were air dried and screened through a no. 850 sieve. Roots were separated, dried, and weighed. Root samples were cleaned and then stained with acid fuchsin in lactophenol to examine mycorrhizal infection. Four 10-g aliquots of screened soil were made from each soil depth sample, and each was placed in a 100-ml graduated cylinder. Ten ml of water were added to wet the sample, and 100 ml of 1-M sucrose solution were added to float spores. After soil particles settled down, the supernatant was poured through a no. 100 (pore size, 150 μm) sieve and was rinsed several times with tap water. This procedure was repeated several times. The materials left on the surface of the sieve were carefully washed into petri dishes for counting and identification. Only those spores appearing to be viable were counted.

Results and Discussion

Sheikh *et al.* (1975) reported that soil at pH 6.2 contains the greatest number of spores of VA-mycorrhizal fungi and that the number decreases with an increase in pH. Results of analysis of soil samples (Table 1) in this study revealed that the pH value was very high, ranging from 9.2 to 10.5, yet the number of spores was also high. Low phosphorus and nitrogen are usually favorable for mycorrhizal development (Gerdemann 1968, Hayman and Mosse 1972). In this study no statistically significant correlations were found between the number of spores and the concentration of soil elements except for sodium. Concentration of sodium was inversely correlated to the number of spores present (≤ 0.05), (Figure 2).

Preliminary examination of roots from grasses indicated heavy VA-mycorrhizal infection in every sample. The predominant species (80 percent of samples) of VA-mycorrhizal fungus was *Glomus mosseae* (Nicol. and Gerd.) Gerd. and Trappe. Next was *Glomus macrocarpum* Tul. and Tul. (<20 percent) and insignificant numbers of spores of *G. macrocarpum* var. *geosporum* (Nicol. and Gerd.) Gerdemann and Trappe, *Acaulospora laevis* Gerdemann and Trappe, and *Glomus fasciculatum* (Thaxter sensu Gerd.) Gerdemann and Trappe.

The population of VA-mycorrhizal fungi in Alvord Desert, based on the number of viable spores counted, varied from averages of 23.7 to 96 spores/g of soil (Table 2). Schwab and Reeves (1981) found that the potential for infection of sage community soil by VA mycorrhizae in western Colorado decreases greatly at depths greater than 30 cm. In this study, no statistically significant differences were detected in the number of spores at each soil depth; however, number of spores is not necessarily related to infection potential. Some samples had decreases in number of spores with increased depth, but others had increases that were presumably due to variations in the microenvironment; for example, soil moisture content and alkali deposit could be affected by differences in microrelief. Nutrient distribution and transformation activities are highly structured in desert ecosystems (West 1981) and result in unequal microbial and chemical activities in the soil horizon. This study indicates that most grasses in their natural habitat, except those in areas under water during the entire growing season, were colonized by some VA mycorrhizae. These highly salt-tolerant VA-mycorrhizal fungi, judging by spore numbers, were apparently not affected by high pH, low soil moisture, nor high soil salinity as evidenced by spore population. The high level of activity by VA-mycorrhizal fungi during periods of moisture availability may be important in nutrient cycling and maintenance of alkali desert plant communities.

TABLE 1. Soil analysis.[2]

Sample no.	pH	P (PPM)	Extractable cations K (PPM)	Ca (meq/100g)	Mg (meq/100g)	Na (meq/100g)	B (PPM)	Salts[2] (mmhos/cm)	Total N (percent)	Cation exchange (meq/100g)	Spore no.
1	9.2	9	2220	47	6.9	21.7	2.92	3.62	0.10	39.8	11.5
2	9.7	7	1560	38	4.6	47.0	4.40	4.50	0.08	36.8	8.0
3	10.1	5	1240	40	2.7	30.0	1.56	4.00	0.05	30.7	10.8
4	10.1	11	2280	38	3.1	45.0	5.55	4.50	0.07	39.9	3.8
5	9.6	7	2860	43	8.9	23.0	4.65	2.22	0.16	42.5	8.8
6	9.4	7	1800	40	6.9	23.1	1.87	1.26	0.11	57.5	5.5
7	10.4	7	1740	34	1.5	64.0	7.00	5.01	0.04	43.2	1.8
8	10.2	8	1360	34	1.9	68.0	3.22	2.98	0.05	45.1	0
9	10.5	7	1160	30	1.1	66.0	5.60	5.10	0.06	50.3	2.8
10	10.4	16	1520	30	1.3	72.0	7.65	13.00	0.05	47.6	0.3
11	10.2	15	2500	35	2.0	47.0	7.25	9.10	0.07	25.6	5.5
12	9.8	8	2220	35	3.1	49.0	3.67	5.70	0.09	43.2	6.5
13	9.4	5	1120	47	6.3	42.0	3.85	5.70	0.04	46.4	7.0
14	9.7	5	1800	38	5.8	5.3	5.65	6.75	0.11	20.5	12.0
15	9.9	7	1520	40	4.5	5.8	7.30	3.12	0.03	40.9	10.5
16	10.2	5	1520	35	2.1	5.7	5.00	3.70	0.04	35.0	11.8

[1]Analysis done by Oregon State University Soil Testing Lab.

[2]U.S. Salinity Laboratory for evaluating saline soils are as follows: conductivity of saturated extracts (mmhos/cm)/plant growth condition: <2—salinity effects mostly negligible; 2-4—yields of very sensitive crops may be restricted; 4-8—yields of many crops restricted; 8-16—only tolerant crops yield satisfactorily; >16—only very tolerant crops yield satisfactorily.

TABLE 2. Correlation coefficients of soil elements and spore number.

Soil element	Correlation coefficient
pH	−0.550
p	−0.516
K	0.133
Ca	0.603
Mg	0.532
B	−0.267
Salt	−0.339
N	0.261
Cation exchange	−0.538
Na	−0.902*

*Significant at $P \leq 0.05$.

TABLE 3. VA-mycorrhizal fungal species, number of species and root mass.

Dominant VAM fungal species	Number of sites	Soil depth (cm)	Mean number of spores g^{-1} soil	Mean root mass $g.g^{-1}$ soil
A. *Festuca idahoensis*				
Glomus mosseae	4	10	69±18	26.6±6.0
		20	54±10	3.0±2.0
		30	53±12	1.3±0.7
		40	48±9	0.5±0.2
G. macrocarpum	3	10	54±7	15.5±3.9
		20	34±6	1.1±0.5
		30	49±12	0.5±0.2
		40	24±5	0.4±0.2
B. *Distichlis stricta*				
G. mosseae	6	10	57±16	11.8±3.4
		20	81±20	1.0±0.8
		30	39±14	0.4±0.2
		40	68±18	0.3±0.2
G. macrocarpum	3	10	96±10	33.7±15.7
		20	71±13	2.9±1.7
		30	46±9	1.2±1.0
		40	44±10	0.7±0.2

Inoculating VA-mycorrhizal fungi capable of increasing salt tolerance in plants will aid in developing new rangeland for animal production from current vast expanses of wasteland. Eventually millions of hectares of the world's high-saline soil could be reclaimed for crop production.

Literature Cited

Gerdemann, J. W. 1968. Vesicular-arbuscular mycorrhizae and plant growth. Ann. Rev. Phytopathol. 6:397-418.

Hayman, D. S., and B. Mosse. 1972. Plant growth responses to VA-mycorrhiza. I. Growth of Endogone inoculated plants in phosphate deficient soils. New Phytol. 70:19-27.

Schwab, S., and F. B. Reeves. 1981. The role of endomycorrhizae in revegetation practices in the semi-arid West. III. Vertical distribution of VA mycorrhiza inoculum potential. Amer. J. Bot. 68:1293-1297.

Sheikh, N. A., S. R. Saif and A. G. Khan. 1975. Ecology of Endogone. II. Relationships of Endogone spore population with chemical soil factors. Islamabad J. Sci. 2:6-9.

West, N. E. 1981. Nutrient cycling in desert ecosystems, pp. 301-304. *In* D. W. Goodal and R. A. Perry (eds.). Arid land ecosystems: structure, function, and management. Vol. 1. Cambridge University Press. Pp. 605.

Received 18 September 1986
Accepted for publication 6 February 1987

S. H. Duncan, J. W. Ward and **R. J. Anderson**
Weyerhaeuser Company, Forest Environmental Sciences
Weyerhaeuser Technology Center, 32901—32nd Drive South, Federal Way, Washington 98023

A Method for Assessing Landslide Potential as an Aid in Forest Road Placement

Abstract

Specific landscape parameters associated with landslides from forest roads were examined in the coast and Cascade ranges of western Washington and western Oregon to develop a slope stability risk assessment technique that can be used by logging engineers as an aid in road location, design and construction in areas of questionable slope stability. Factors relating to slope stability were examined on 4,266, 61-m road segments covering 260 km of road in five physiographic areas. Using stepwise discriminant function analysis, the sum of scores representing nine individual slope stability variables resulted in a classification between fail and no-fail sites at 88 and 66 percent accuracy, respectively, at the 0.01 level of confidence. By adjustment of individual weighting values, the qualitative technique presented here can be adapted to other areas to assess landslide risk.

Introduction

Landslides associated with forest roads have been recognized by Brown and Krygier (1971), Dyrness (1967), Swanston and Dyrness (1973), and many others as the major sources of sediment from the managed forests of the Pacific Northwest. Studies conducted throughout the Pacific Northwest have identified the need for better road location, harvest unit design, and engineered road construction, as well as timely and appropriate maintenance in order to reduce accelerated soil mass movement and stream sedimentation in forested watersheds.

Transfer of applicable geological and geotechnical information into practice is often difficult since the expertise required to assess slope instability, and apply the appropriate technology, is too expensive or technically impractical for many field engineers or small operators in the private sector.

There are various methods used to assess potential slope instability. Mathematical models depicting site specific slope stability as presented by Terzaghi (1950) can be used but are impractical in most forest road applications. Qualitative systems of slope stability classification are commonly applied by geologists in mapping landslide hazard sites, but the techniques lack the site specificity often required by the logging engineer. An attempt to blend the qualitative with a quantitative output was attempted by McNutt (1975) who presented a series of probabilistic slope failure equations developed through analysis of a series of questionnaires completed by knowledgeable scientists and engineers. The type of model resulting from this analysis is extremely cumbersome to use in field application.

Swanston *et al.* (1979) presented a slope stability assessment and sediment delivery technique in which specific landscape parameters are assigned relative weighting values. In application, each parameter is identified, the values summed and a qualitative assessment of the potential stability of a site determined. Although this technique identifies key elements in the stability of forest slopes, it was not subjected to analytical testing. Quantitative analytical methods to assess slope stability for specific geologic terrain in northern California were presented by Rice and Pillsbury (1982), and Furbish and Rice (1983). Similar analytical methods were used by Muscato (1975).

The slope stability technique presented here blends the qualitative methodology of Swanston *et al.* (1979) and the quantitative analytical methods described by Rice (1967). Because of the complexity of the interaction of hillslope processes and microclimatic effects in forested watersheds of the Douglas-fir region, models that use analytical techniques to verify estimates of qualitative parameters are about as precise as is practical. Care must be exercised in application of such models beyond the area of development since they may misrepresent the operation of local processes.

This paper discusses a slope stability assessment technique for field application by the logging engineer with a general level of knowledge

in geologic and soil sciences. The technique can aid in making decisions concerning road location, design and construction in terrain of questionable stability, and assist in assigning road maintenance priorities. Through its application, the technique also serves as an educational aid where the hillslope is examined and interpreted differently than in standard engineering practice. This stability assessment technique is not an erosion prediction system but a tool to aid the engineer in assessing the stability potential of the hillslopes likely to be encountered.

Methods

The study area (Figure 1) contained sufficient geologic, topographic and climatic diversity that a selection of study sites representative of the various physiographic conditions was essential to identify adequately landscape factors associated with road related landslides. Site selection and evaluation was accomplished in two phases: 1) a broad sampling of representative geologic conditions and associated forest harvesting operations, and 2) a site specific sample where select sites identified in the broad sample process were chosen for more detailed study.

Broad Based Sample

Lands owned by Weyerhaeuser Company and intervening public lands west of the Cascade mountains between the Snohomish River in Washington and the Millicoma River in Oregon were divided into five physiographic Provinces: 1) foothills of the northern Washington Cascades, 2) southwestern Washington Cascades, 3) west-central Oregon Cascades, 4) Washington coast range, and 5) Oregon coast range. Each physiographic area was further separated by the predominating geology and climate. Areas where slope failure is extremely rare, such as the broad, low-lying glacial plains of the Puget Sound basin, were eliminated.

Township-centered aerial photographs at a scale of 1:64,000, in combination with geologic maps, were found to be most useful in identification of major landforms and the level of associated landslide and forest harvesting activity. In clearcut areas, landslides of approximately 0.75 to 1 acre in size can be identified and debris torrent paths are clearly evident. Although this photo scale did not allow accurate identification in timbered areas or identification of small soil disturbances, the general frequency of landsliding associated with specific physiographic form allowed selection of representative sites and their associated landslides.

Identifiable mass failures associated with forest roads were recorded for each province on the township-centered aerial photographs. In order to cover a wide range of climatic events, photographs taken in 1972, 1974 and 1978 were used. During this time period, recorded storm events ranged from less than the annual event to that equaling the 100-year storm in several watersheds in the study area. A total of 921 road-related failures were identified in this examination.

For each failure site, the parameters of slope angle, slope position, slope form and stand age were identified and slope angle in groupings of $<22°$, $22°$-$31°$ and $>31°$ were estimated by photo-interpretation. Additional parameters such as soil type and elevation were obtained for each site from soil survey maps overlaid on a topographic base. Each failure site was numbered and a 10 percent random sample chosen for field examinations in which specific variables were checked for accuracy. Frequency plots were then made for each variable by physiographic province.

From these data relative weighting values were assigned to each stability variable. For example, failure frequency associated with slope angle was found to increase exponentially with failures approximately eight times more frequent at slope angles in excess of 35° than between 12° and 22°. In this manner a preliminary table for slope stability assessment, similar to Table 1, was constructed. Each weighting value was considered to represent the relative contribution of the individual variables to slope stability. Weighting values ranged from -10 for a ridge top slope position to $+8$ for a slope angle in excess of 35°. An in-depth description of the importance of each of the primary slope stability variables used in this study is given by Swanston (1981).

The stability assessment table developed from this analysis follows the form presented by Swanston *et al.* (1979). Swanston's system consists of two assessment tables, one to be used in areas where shallow planar landslides are the dominant feature, and one for slump-earthflow

Figure 1. Location of the study area

TABLE 1. Slope stability index rating table

Factor	Description	Numerical Value
Slope Angle	• ≥71% (≥35°)	8
	• 57-70% (30°-35°)	6
	• 40-56% (22°-30°)	3
	• 20-39% (12°-22°)	1
	• <20% (<12°)	−4
Slope Position	• Upper third	3
	• middle third	2
	• Lower third	1
	• Ridge or bench	−10
Slope Form	• V-notch drainage	5
	• Concave slope	4
	• Straight slope	2
	• Convex slope	1
Soil Depth and Subsoil Texture	• Cohesive: clay, clay loam and loam or silt loam >20% clay	
	Depth <20" (<51 cm)	4
	20-40" (51-101 cm)	3
	>40" (<101 cm)	5
	• Non-cohesive: sand, loamy sand, sandy loam and loam or silt loam <20% clay	
	Depth <20" (<51 cm)	5
	20-40" (51-101 cm)	2
	>40: (>101 cm)	1
Bedrock Type	• Volcanic rock —Highly weathered (soft, easily disintegrated) —Hard, relatively unweathered, massive	4
	• Sedimentary rock —Siltstone, shale and soft (weathered) sandstone —Hard, relatively unweathered sandstone	
	• Unconsolidated deposits —Sand, silt and clay (glacio-fluvial) —Ancient landslide materials	
	• Hard impervious glacial till	
	• Volcanic rock—highly fractured and jointed with zones of deep weathering, or interbeds of sedimentary or volcano-clastic material	3
	• Volcanic rock—hard (relatively unweathered) but highly fractured and jointed	2
Groundwater	• Permanent springs or seepage areas	3
	• Seepage or spring present during winter months	2
	• No evidence of groundwater emergence	1

(continued on next page)

TABLE 1. Slope stability index rating table, continued

Factor	Description	Numerical Value
Elevation	• Cascade foothills and Puget-Willamette lowlands	
	— ≤1000 (≤305 m)	1
	— 1100-2000 (335-610 m)	2
	— 2100-2900 (640-884 m)	4
	— ≥3000 (≥915 m)	2
	• Coastal Mountains	
	— <1000 (≤305 m)	3
	— ≥1000 (≥305 m)	4
Road Placement	• Terrain of former failure:	
	— Toes of ancient slumps and earthflows — Slump scarps (headwalls) — V-notch drainages with bedrock channels or large alluvial fans	8
	• Naturally critical terrain: — Slope >57% (30°) •• Side and headwalls of narrow V-notch drainages Concave depressions — Slope >40% (22°) •• Bench edges or abrupt slope breaks	4
	• Apparently stable terrain: No evidence of former failure activity or critical terrain features	1
Stand Age	<10 years	3
	≥10 years	1

terrain. While a separate assessment for each condition is a valid approach, we determined that for any technique to be readily accepted and used in the field, it must be as easy to use as possible. In testing the Swanston model we discovered that there could on occasion be confusion in determining which assessment table was appropriate, therefore we chose to develop a single table that would assess the relative potential of a site to fail by sliding after road construction. To avoid the possible influence of extraordinary road construction techniques, such as end hauling of waste soil material, all the sites evaluated had roads that were located and constructed according to standard forest road construction practices.

Site Specific Sampling

To ensure uniform sampling throughout each province, soil survey reports (Steinbrenner and Gehrke 1964, 1966; Steinbrenner and Duncan 1969, Duncan and Steinbrenner 1971, 1972; Duncan *et al.* 1973; Webster and Steinbrenner 1974) were used to identify soil associations.[1] Area in each association was determined and the number of individual study sites chosen according to the weighted area. This resulted in 134 50-ha sites. To ensure as much control as possible over natural variation, four conditions for site selection were required: 1) each site was within the boundaries of the same photographic project; 2) all sites were roaded; 3) each site included a mix of stand ages, and 4) a uniform sampling of the slope angle, topographic forms and elevational ranges representative of each geologic province was included. The 50-ha size furnished an area

[1]A soil association was defined as a grouping of soils occurring in the same physiographic and climatic area and forming from similar geologic materials.

containing a sufficient amount of road of various ages to allow a statistically representative sample. Each site was then delineated on 1:12,000 scale aerial photographs, all haul roads within the site boundary were divided into 61-m segments, existing landslides recorded and stability variables assigned to each segment by photo-interpretation (Table 1). The 134 40-ha sites included 4,266 individual 61-m road segments totaling 260 km of road.

Each site was visited to verify the parameters identified on the photos. As a result of this detailed examination, three additional variables were added to the assessment table. A variable recognizing the presence of perched ground water was added, as well as a variable that would identify the specific placement of the road on the hillslope in relation to terrain features considered to be critical to slope stability after road construction. A more accurate representation of climate was determined by examination of failures by elevation zones in each province. As a result failures in the Cascades were found to be four times more prevalent in the elevation zone between 640 and 884 M elevation than at lower elevations. A similar trend was seen for the upper elevations in the coast ranges. It is suggested that the primary reason for the increase in landslide activity in these elevation zones is the occurrence of rain-on-snow events. Although boundaries of the rain-on-snow zone change somewhat with latitude across the study area, the 640 to 884 M zone in the Cascades and the area above 305 M in the coast range has been found through our watershed monitoring activities and forest operations to be the most critical for this type of event. The elevation variable was used as a climatic index.

Data were divided into two groups: 1) those road segments where failure had occurred, and 2) those segments that had not failed. Because road failures are often the result of inadequate road maintenance, and in this analysis we were interested in assessing the linkage between road construction and primary hillslope elements in regard to site stability, failures directly related to neglected road maintenance were eliminated from the analysis when this cause could be identified. The numerical values representing the individual stability variables for each segement by group were examined by stepwise discriminant function analysis as used by Muscato (1975).

Discriminant function analysis was first performed on all stability variables for each road segment by province. Since no significant difference could be determined between provinces, it was assumed that variation between areas had been accounted for in variable identification; all data were combined for further analysis.

Results and Discussion

It was determined at the beginning of this study that to be truly useful, a slope stability indexing system must be capable of an accuracy of at least 80 percent with a 95 percent level of confidence and be easy to apply in practice. When each of the nine variables—slope angle, slope position, slope form, soil characteristics, bedrock type, groundwater, elevation, road placement and stand age—were examined in combination they yielded a fail, no-fail classification accuracy of only 55 percent. Classification accuracy was increased to 70 percent by adustment of individual weighting values and elimination of the critical terrain portion of the road placement variable as a possible source of bias since it could result in a double weighting of slope angle and slope form. Although the fail, no-fail classification was significant to the 95 percent level of confidence, the model was cumbersome to operate using nine individual variables and its accuracy was short of the 80 percent goal.

Because of the significance of the individual variables, it was hypothesized that the sum of the variables could be considered to represent an index of stability for each site. This would also increase ease of use. This sum was termed the "stability index." To test this hypothesis, all sites were then analyzed using the sum of all nine original variable values as a single value (stability index) for each of the 4,266 data points. The result of this analysis yielded a correct assignment of 88 percent for the failed group and 66 percent for the no-fail group and was significant at the 99 percent level of confidence. The analyses were completed with development of the following equation:

$$\text{Failure Risk} = 3.6236 + 1.0787\ (\text{index}) + 0.034287\ (\text{index})^2$$

The consistency of the stability index between photo-interpretation and on-site evaluation was determined by field verification. A random 10

percent sample of the data points were chosen for field examination. Sites were separated into fail and no-fail groups and visited for determination of stability variables. Since presence or absence of ground water seepage, precise estimation of slope angle and soil parameters can only be approximated by photo-interpretation, these factors were the ones most often changed in field evaluations.

Data for each road segment in the verification sample were arranged into a photo group (photo-interpreted factors from original analysis) and a field group (on-site-determined factors from verification examination), the groups separated into fail and no-fail categories as previously described, and the statistical analyses performed as before.

Prediction accuracy was slightly better for field-evaluated sample points than the photo-interpreted group. Using the sum of all nine stability variables (the stability index) prediction accuracy for the field group exceeded 85 percent. The photo-interpreted group had a prediction accuracy between 80 and 91 percent. All predictions were within the 80 percent accuracy specified.

This particular slope stability indexing technique, like those developed in other areas, is somewhat unique to a particular range of geologic and climatic conditions. Because of this, each technique must be considered as having limited geographic application. Although this model may be adapted to other areas through adjustment of the individual numerical weighting values, rigorous testing would be required. Land managers are therefore cautioned in general application and extrapolation outside of the area in which the particular model was developed.

Application

In application, each of the factors in Table 1 are determined for the proposed station of road and their values summed to obtain the stability index. Failure risk for the average road is estimated by relating the stability index to the risk curve in Figure 2. For ease of interpretation, the indices have been grouped into the following classes of potential instability: low, −7 to 15; medium, 16 to 24; high, 25 to 31; extreme, 32 to 42.

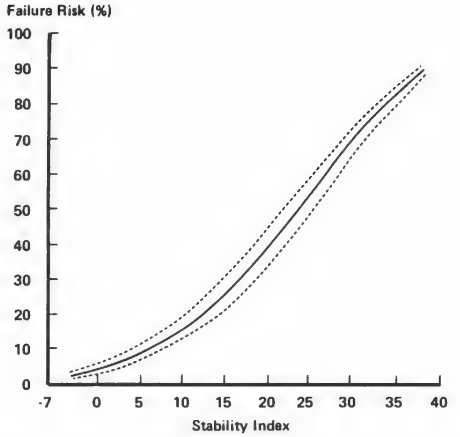

Figure 2. Relationships of failure risk to the slope stability index.

This technique of indexing slope failure potential was originally developed in 1979 as an educational aid. Subsequently, the technique has been programmed as a subroutine to a Company-owned, computer-assisted logging, engineering and road design module and has been used by Weyerhaeuser Company engineers as an aid in locating new roads and landings in areas of questionable slope stability. The authors have examined the use of the model in identifying and prioritizing sites along existing roads where more intensive maintenance or reconstruction may be required to reduce the potential of slope failure. Although the sample was small compared to the original data set, the results were promising.

It is unknown what effect application of this system has had on failure frequency. Since its implementation, an increased awareness of soil and geological parameters among field engineers has been evident, resulting in higher design standards and construction practices in areas with high slope failure potential.

Literature Cited

Brown, G. W., and J. T. Krygier. 1971. Clearcut logging and sediment production in the Oregon Coast Range. Water Resour. Res. 7:489-498.

Duncan, S. H., and E. C. Steinbrenner. 1971. Soil survey of the St. Helens tree farm. Weyerhaeuser Co., Western Forestry Research Center, Centralia, WA 98531.

_____. 1972. Soil survey of the Calapooya and Millicoma tree farms. Weyerhaeuser Co., Western Forestry Research Center, Centralia, WA 98531.

Duncan, S. H., S. R. Webster, and E. C. Steinbrenner. 1973. Soil survey of the White River tree farm. Weyerhaeuser Co., Western Forestry Research Center, Centralia, WA 98531.

Dyrness, C. T. 1967. Mass soil movement in the H. J. Andrews Experimental Forest. USDA For. Serv. Res. Pap. PNW-42 Northw. For. and Range Exp. Sta., Portland, Oregon. 12 pp.

Furbish, D. J., and R. M. Rice. 1983. Predicting landslides related to clearcut logging northwestern California, U.S.A. Mountain Res. Develop. 3:253-259.

McNutt, J. A. 1975. A stochastic analysis of erosion and economic impacts associated with timber harvest and forest roads. Oregon State University, Corvallis. Ph.D. Dissertation.

Muscato, D. I. 1975. Computer and statistical analysis of landslide impact on granitic terrain. Cal. Polytechnic College, San Luis Obispo. M.S. Thesis.

Rice, R. M. 1967. Multivariate methods useful in hydrology. Proc. International Hydrology Symposium, Fort Collins, Colorado. September 6-8. 1:471-478.

Received 30 April 1986
Accepted for publication 18 February 1987

Rice, R. M., and N. H. Pillsbury. 1982. Predicting landslides in clearcut patches. *In:* Walling, D. E. (ed.), Recent developments in the explanation and prediction of erosion and sediment yield. Proceedings Exeter Symposium IAHS Publ. No. 137.

Steinbrenner, E. C., and S. H. Duncan. 1969. Soil survey of the Clemons tree farm. Weyerhaeuser Co., Western Forestry Research Center, Centralia, WA 98531.

Steinbrenner, E. C., and F. E. Gehrke. 1964. Soil survey of the Vail tree farm. Weyerhaeuser Co., Western Forestry Research Center, Centralia, WA 98531.

_____. 1966. Soil survey of the McDonald tree farm. Weyerhaeuser Co., Western Forestry Research Center, Centralia, WA 98531.

Swanston, D. N. 1981. Watershed classification based on soil stability criteria. *In:* Baumgartner, D. (ed.), Interior West Watershed Management Symposium Proc., Washington State University, Pullman. Pp. 43-58.

Swanston, D. N., and C. T. Dyrness. 1973. Stability of steep land. J. For. 71:264-269.

Swanston, D. N., F. J. Swanson, and D. Rosgen. 1979. Prediction techniques for determining potential changes in sediment contributions from mass wasting processes due to silvicultural activities. *In:* Water resources evaluation, non-point sources, silviculture (a procedural handbook): EPA-600/8-80-012. Pp. Vi-V46.

Terzaghi, K. 1950. Mechanism of landslides. *In:* Paige, S. (ed.). Application of geology to engineering practice. Berkey Vol. GSA. Pp. 83-123.

Webster, S. R., and E. C. Steinbrenner. 1974. Soil survey of the Snoqualmie Falls tree farm. Weyerhaeuser Co., Western Forestry Research Center, Centralia, WA 98531.

A. B. Adams, V. H. Dale[1], Botany Department, University of Washington, Seattle, Washington 98195

E. P. Smith[2], Center for Quantitative Science
University of Washington, Seattle, Washington 98195

and

A. R. Kruckeberg, Botany Department, University of Washington, Seattle, Washington 98195

Plant Survival, Growth Form and Regeneration Following the 18 May 1980 Eruption of Mount St. Helens, Washington

Abstract

The composition of plant communities changes after cataclysms such as volcanic eruptions. These community changes might be more accurately forecast if the floristic composition of communities is known prior to an eruption because recovery of plants depends upon the mechanisms by which they normally respond to disturbances. To identify some of these mechanisms and their consequences for plant community recovery, we followed the recovery of plant communities after the 18 May 1980 lateral blast of Mount St. Helens and examined both species that survived and those that regenerated. Plants with subterranean dormant buds (geophytes) and those that could regenerate from fragments survived the eruption best. As a result, the proportion of geophyte species and relative plant cover of geophytes was significantly higher than that of other growth form types. Initial recruitment onto the hummocky-surfaced debris slide (i.e., mounded-surface) was strongly biased toward geophytes and annuals, possibly due to extreme environmental conditions on this new substrate. In contrast, other habitats (blowdown, mud flow and scorched, dead forest) created by the eruption have higher vegetation cover and are dominated by plants that survived the eruption. Because plants have evolved in response to frequent disturbances such as fires, snowslides and floods, they are preadapted to similar, but less frequent, disturbances that are associated with volcanic eruptions.

Introduction

After large-scale ecosystem disturbance accurate assessments of plant regeneration are necessary for determining resource availability for terrestrial and aquatic fauna, estimating the quantity of sediment to be expected downstream, and assessing the magnitude of competition that commercial plantations may encounter. The effects of volcanic disturbances on plant communities and the importance of growth forms in plant reestablishment have been described (Smathers and Mueller-Dombois 1974, Man'ko 1974, Griggs 1933, Franklin *et al.* 1985, Antos and Zobel 1985a,b). The pre-eruptive influence of climate and recurrent disturbances such as fires, floods, and snowslides have been recently considered as selective agents of adaptations that increase the probability of surviving eruptions (Adams and Dale 1987, Antos and Zobel 1985a,b). A variety of plant responses to burial have been described by Antos and Zobel (1987) including the formation of adventitious roots, upward growth of rhizomes, and movement of perennating buds.

Influences of climate, time, and substrate have been formulated in a predictive model for long-term biomass accumulation on lava substrates by Eggler (1971). Halpern and Harmon (1983), based on initial observations of revegetation of the Lower and Upper Muddy River mud flow at Mount St. Helens, predicted successional patterns to be variable following this volcanic disturbance because there is a variety of surface substrates for colonization, means of reproduction and distances to seed source. Differential plant survival within and between disturbance types has not been statistically tested after past debris avalanches and associated lateral venting of stratolayer volcanoes such as those that occurred at Bandai-san, Japan, in 1888 (Sekiya and Kikuchi 1889), and at the Russian volcanoes Bezymianny in 1956 and 1964 (Tokarev 1981). Griggs (1933) working four years after the 1912 eruption of Mount Katmai, Alaska, noted both the importance and difficulty in differentiating between hold-over plants and new colonizers following volcanic eruptions.

The eruptions of Mount St. Helens, Washington (Lipman and Mullineaux 1981, Swanson *et al.* 1983, Weaver *et al.* 1983, and Waitt *et al.* 1983), provide opportunities to develop methods for predicting the mechanisms and magnitude of

[1]Current address: Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee, 37831.
[2]Current address: Statistics Dept., Virginia Polytechnical Inst. & State University, Blacksburg, Virginia, 24061

vegetation recovery following cataclysmic eruptions. Since quantifying differences in plant growth forms would allow us to substantiate or refute past observations for vegetation following other volcanic eruptions and provide a means for assessing future successional trends, we decided to use the Mount St. Helens blast zone to test for differential survival as a function of growth form. By looking in the time period immediately following the lateral blast, we were easily able to separate hold-over plants from new colonizers. We believe that the methods and results presented in this paper provide a simple way of using pre-eruptive plant composition and associated types of plant regeneration for forecasting potential plant recovery in the aftermath of a large-scale natural disaster.

Methods

Sampling within Disturbance Habitats

The post-eruptive habitats selected to examine differences among growth forms were: 1) blowdown; 2) standing scorched (seared), dead forest; 3) mud flow; and 4) debris avalanche (Figure 1). Ocular estimates of percent cover by species (obtained by dividing the plots into quarters and summing to give a total estimate for each plot), the number of species above the ash, phenological stages (seedling, emerging, immature plant, flowering, setting seed or dead) represented by each species, ash depth and distance from the crater were recorded for 25 m^2 circular plots from late June to August of 1980 in blowdown and scorched, dead forests, and mud flow habitats. Because plant cover was markedly lower on the debris slide relative to the other three habitats considered in this research, we predicted that plant establishment onto the debris would be related for the most part to survival of seedlings. This would allow a contrast of growth forms in a habitat recolonized by seeds with habitats in which a greater proportion of the flora survived. Therefore, we considered annual and seasonal variability in growth forms on the debris slide by sampling over a three year period (15, 83 and 103 250 m^2 permanent circular plots during August of 1980, 1981, and 1982, respectively) and for three time intervals during the summer of 1982 (June, July and August). In addition to the information collected for the plots in the other three habitats, for the debris slide plots we recorded the number of stems/species at the soil surface.

Growth Form Classification and Spectra

Plants were classified by the location of dormant meristematic tissue relative to the ground surface (Raunkiaer 1934, Mueller-Dombois and Ellenberg 1974). Growth form spectra were constructed for species classified as annuals (A), plants with buds below ground (G or geophytes), plants with buds at the ground surface (H or hemicryptophytes), plants with buds 2.5 to 50 cm above the surface (C or chamaephytes), tall shrubs (S), deciduous trees (D) and evergreen trees (E). The percent of species for pre-1980 data (256 spp.) was constructed using the data of St. John (1976). The growth form spectra of percent species for the four disturbance habitats were determined using species lists constructed on forays through the habitats and from established plots. The percent cover of growth form types averaged for the total area was determined by summing the average cover of each growth form within a given habitat and then dividing this sum by the total number of habitats. The cumulative mean number of individuals per plot was calculated by dividing the total number of individuals of each growth form by the number of plots and summing the growth forms for each sampling period.

Analysis of Types of Plant Regeneration

Three types of regeneration were considered in our field work: 1) regeneration from newly deposited seeds (recruitment or establishment of new genets); 2) regeneration from *in situ* surviving plants; and, 3) regeneration from plant fragments transported by the energy forces associated with the eruption (e.g., the blast, avalanche and mud flows). The presence of seeds was documented with seed traps (0.25 m^2) (Adams and Adams 1982, Adams and Dale 1987). Seedlings were distinguished from emergent residual plants by the presence of cotyledons and the absence of subterranean tissue from previous years' growth. Plants were unearthed to determine if regeneration was occurring from fragments or from *in situ* rootstocks sprouting in mineral soil. To ascertain the potential of subalpine lupine (*Lupinus latifolius*) to regenerate vegetatively, a single lupine rootstock was placed

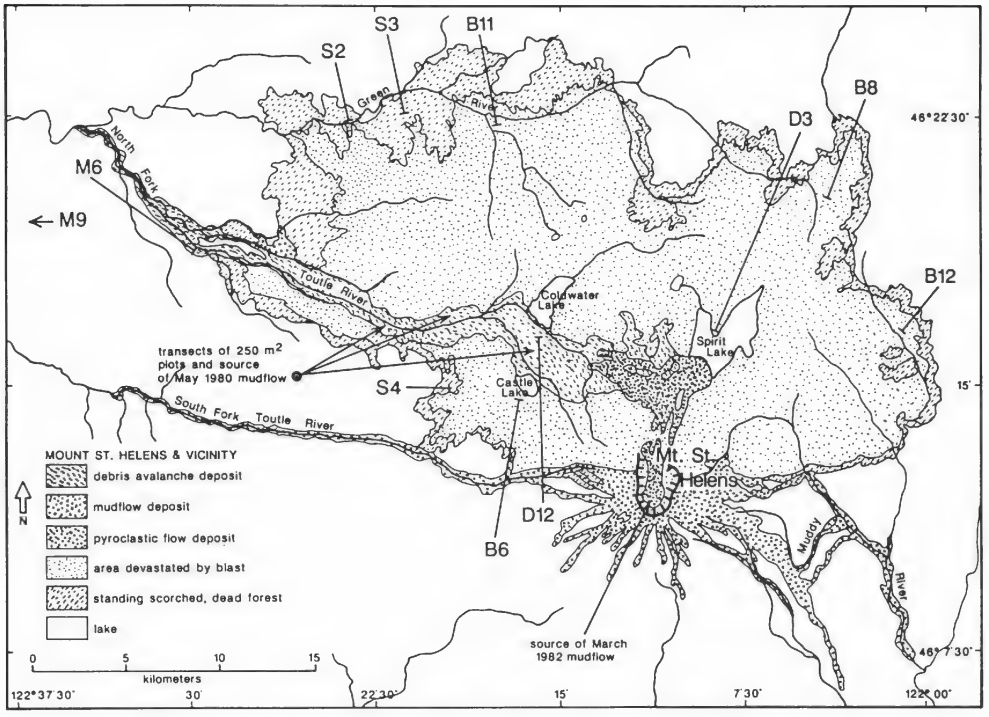

Figure 1. Map of study area relative to the confluence of the Cowlitz and Toutle Rivers and the Mount St. Helens crater. The location of 25 m^2 circular plots and transects in 4 disturbance habitats are shown. The bold letters indicate the disturbance type and the associated numbers denote the number of plots at each location. Disturbance types are blowdown (B), standing scorched, dead forests (S), mud flows (M) and debris slide (D). The set of plots designated M9 represents 9 plots located west of the map approximately 1 km east of the confluence of the Cowlitz and Toutle Rivers. The 250 m^2 permanent circular plots on the debris slide used in 1980 ran south to north from Castle Lake to Coldwater Lake and 3 plots were located on portion of the debris slide that splashed across Spirit Lake and was deposited just north of Spirit Lake. In 1981 and 1982 the plots ran from 5 km east of the terminus of the debris slide to Castle and Coldwater Lakes. Plots are spaced at 50 m intervals along line transects in all habitats.

in six clay pots filled with debris substrate and the rootstocks were watered daily at the University of Washington greenhouse. Methods used to determine substrate physical and chemical properties, and moisture stress troughs used in documenting regeneration from transported fragments are described in Adams and Dale (1987).

Statistical Analyses

To test the significance of distance relative to ash depth in residual plant recovery, a multiple regression was run utilizing number of species as the dependent variable versus ash depth and distance as the independent variables. To determine the significance of differences in abundance of growth form types, a two-way ANOVA with unequal frequencies was performed on the log transform (Y + 0.0005) of percent cover with growth form and disturbance type as factors. For the debris slide data collected in permanent 250 m^2 circular plots during August of 1980, 1981, and 1982, a two-way ANOVA with unequal frequencies was performed on the log transform of number of individuals with growth form and year as factors. Significant differences between growth form types were determined by computation of Scheffe's pair-wise contrast tests (Winer 1971).

Results

Similarities and Contrasts in Growth Form Spectra of the Four Habitats

Disturbance types had different growth form spectra (Figure 2) and different types of plant regeneration. Annuals were poorly represented in the pre-eruption flora and were absent from all four habitats in the summer subsequent to the eruption of Mount St. Helens (Figure 2A). All six other growth form types were represented by residual or surviving species. The relative proportion of geophytes was higher for the total area than existed in the pre-1980 flora, whereas hemicryptophytes and chamaephytes are notably less. No major changes in the relative proportions of species of tall shrubs, deciduous or evergreen trees were noted when the spectrum for the pre-1980 flora is compared with the cumulative percent of species for the total.

Growth form spectra of cumulative percent of species were similar for blowdown and scorched, dead forests, but these two spectra differed from those that occurred on lahars (mud flows and the debris slide) (Figure 2A). Since species compositions were identical for blowdown and dead, scorched forests (100 spp.), these spectra are presented as a single spectrum in Figure 2A. In the blowdown and scorched, dead forests, above-ground plant tissue was removed by the lateral blast. Here most plants regenerated *in situ*. Over 70 percent of these species and 89 percent of the relative cover consisted of plants with perennating buds below the ground. The mud flow (22 spp.) and debris slide (20 spp.) habitats differed from the blowdown and scorched, dead forests by the occurrence of relatively fewer geophytes. The mud flow differed from the debris slide spectra by having a higher proportion of species that have buds projecting above the mud's surface (shrubs >50 cm, deciduous and evergreen trees) and fewer species with buds below the surface.

The barplots of each separate habitat represent the cumulative sum of the means of each growth form type (Figure 2B). Total mean percent cover was low in all four habitats ($\leq 25\%$), but nevertheless higher than we had expected. Plants with buds below the surface represented the highest percent cover/plot, followed by deciduous and then evergreen trees. A two-way ANOVA utilizing percent cover with growth form and disturbance type as factors, showed that the growth form-disturbance type interaction was significant ($p < 0.001$, $F_{15,48} = 8.02$). Computation of pair-wise contrast tests indicated that the main differences were associated with the relative importance of conifers and deciduous trees on the mud flow and geophytes in other disturbance types. In 1980, percent cover for hemicryptophytes and trees was low; nevertheless, cover was 16 times higher for plants with buds at the surface and twice as high for trees in the scorched, dead forests than in the blowdown.

Mechanisms of Regeneration

In 1980 survival of seedlings was found to be virtually nonexistent in all four habitats (Adams and Adams 1982). In 1980 regeneration in the blowdown and scorched, dead forests was almost entirely from *in situ* plant parts sprouting from mineral soil. No regeneration from transported plant fragments was found in these two habitats. The number of species regenerating seemed to be related to erosion in that the greatest number of species were found on moderately steep slopes

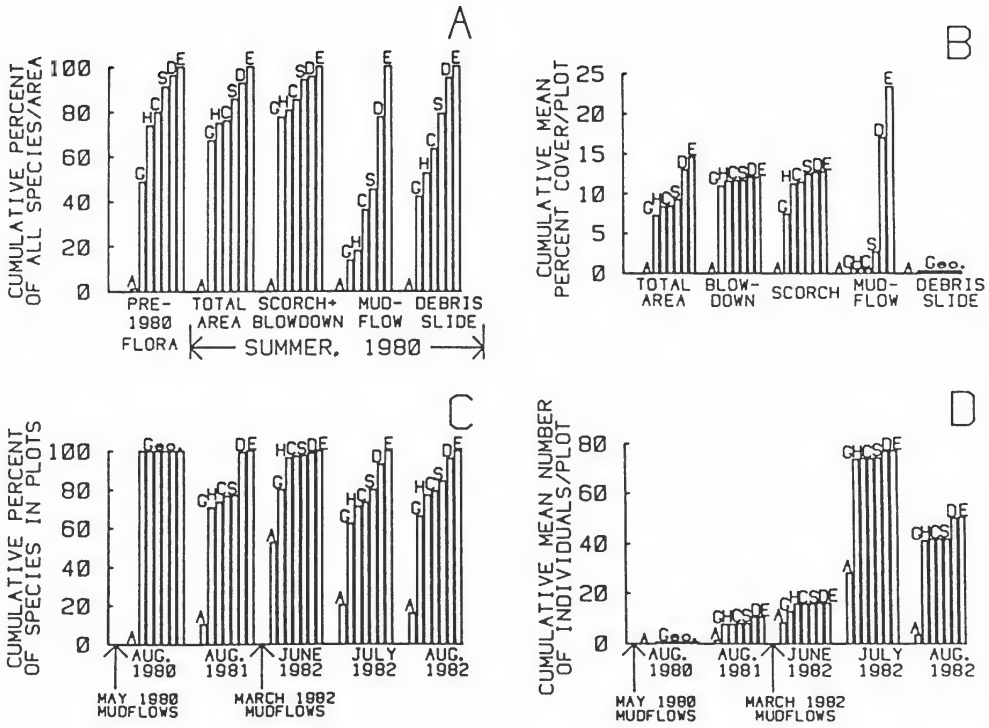

Figure 2. Growth form spectra are reported for species classified as annuals (A), plants with buds below ground (G), plants with buds at the ground surface (H), plants with buds 2.5 to 50 cm above the surface (C), tall shrubs (S), deciduous trees (D) and evergreen trees (E). (A) The percent of species for pre-1980 data (256 spp.) (St. John 1976) and for 4 disturbance habitats sampled from June to July, 1980. (B) The percent cover of growth form types averaged for the total area (sum of average cover of each habitat divided by the total number of habitats) and for the 4 disturbance types for 25m² circular plots sampled during July and August of 1980. (C and D) Growth form spectra for 250m² plots located on the debris slide. (C) Cumulative percent of species in debris avalanche plots. (D) Cumulative mean number of individuals per plot calculated by dividing the total number of individuals of each growth form by the number of plots and summing the growth forms for each year. On 19 March 1982 an explosive eruption generated a lahar that covered a large portion of the debris slide as far as 8 km from the crater (Waitt *et al.* 1983). This secondary disturbance is noted on Fig. 2C-D.

with gullies that penetrated through the ash to the surface of the pre-eruptive mineral soil. Multiple regression of data from blowdown and scorched, dead forests shows number of species (N)/25 m² plot surviving and emerging above the ash in July 1980 to be related to depth of ash (D in cm), and not to distance from the mountain ($N = 5.75 - 0.22D$, $p = 0.002$, $r^2 = 0.40$, $n = 50$ plots); [addition of distance increases r^2 by 0.005 and the coefficient is not significantly different from 0 ($p = 0.620$)]. Regeneration from *in situ* geophytes and hemicryptophytes was rare on both the mud flow and debris slide. Regeneration from transported fragments occurred throughout the North Fork Toutle mud flow sites. On the debris slide vegetative regeneration was mostly in tributary backfills and the outer margins of lateral terraces (Voight *et al.* 1981) associated with rootwads, clumps of mineral soil and distal clumps of forest fragments deposited at the western terminus of the slide.

On the North Fork Toutle mud flow and debris slide more than 20 species regenerated from fragments and from plants transported on root wads, stumps and soil torn from the valley walls. Regeneration occurs from tubers [western starflower (*Trientalis latifolia*)]; corms [trillium-leaved wood-sorrel (*Oxalis trilliifolia*)]; rhizomes [beargrass (*Xerophyllum tenax*)]; and taproots [pearly everlasting (*Gnaphalium microcephalum*)]. In 1980, on the debris slide, fireweed (*Epilobium angustifolium*), Canadian thistle (*Cirsium arvense*) and lady fern (*Athyrium filix-femina*) sprouted from axillary buds of transported rhizomes. In mud flow material of the North Fork Toutle valley located four km west of the debris slide terminus up to five fragments were found sprouting within a 25 m² plot in 1980 [Mertens' sedge (*Carex mertensii*), dagger-leaf rush (*Juncus ensifolius*) and horsetails (*Equisetum* spp.) from rhizomes]. Broken branches of black cottonwood (*Populus trichocarpa*) and willows (*Salix* spp.) developed leaves and stems from preformed primordia embedded in bark on stem sections on both the mud flow and debris slide. Nine fragments [soft rush (*Juncus effusus*), *C. mertensii* and bentgrass (*Agrostis diegoensis*)] sprouted from mud flow substrate spread over an area of 13 m² as part of a moisture stress trough experiment conducted within the University of Washington research greenhouse (Adams and Adams 1982, Adams *et al.* 1986). *Lupinus latifolius* became established on the debris slide and set seed in 1981. All six rootstock sections of this lupine placed in debris substrate sprouted shoots and roots within two weeks.

Yearly and Seasonal Trends on the Debris Slide

Only geophytes were found in the debris slide plots in 1980 and geophytes remained predominant in August samples during the three year study period. With the exception of small shrubs, all growth forms showed relative increases in importance to the total spectra subsequent to 1980. Yearly changes in cumulative percent of species in 250 m² circular plots on the debris slide were pronounced (Figure 2C). In particular, the proportion of annuals and deciduous trees increased.

Although total plant cover remained less than one percent on the debris slide through 1982, there were three orders of magnitude increase in the number of individuals/250 m² plot from 1980 to 1982 (Figure 2D). The two-way ANOVA with unequal frequencies performed on number of individuals with growth form and year as factors was significant ($p < 0.001$, $F_{20,203} = 13.21$). The interaction of growth form with year was insignificant. Contrast tests indicate the main difference is due to the increase of plants with buds underground, and to a lesser degree to the change in annuals, and to an even smaller increment of increase from deciduous trees.

In 1982 the total number of plants on the debris slide increased from June to July and then decreased from July to August (Figure 2D). Deciduous trees in 1982 showed an increase throughout the sampling period but represented < 10 percent of the total number of individuals. Annuals and geophytes show the largest increases from June to July of 1982, whereas annuals decrease and geophytes remain unchanged from July to August. As expected, over 99 percent of the increase in numbers of individuals on the debris slide was from seed dispersal and seedling survival during 1981-82 as was easily determined by the presence of cotyledons and lack of tissue from previous years' growth.

Discussion and Conclusions

General Features of the Growth Form Spectra

The structure of flora surrounding Mount St. Helens both before and after 1980 is distinguished from other vegetation at temperate latitudes of the northern hemisphere as described by Whittaker (1960), and differs from nearby volcanoes such as Mount Rainier, Washington, by a high proportion of geophytes relative to hemicryptophytes and chamaephytes. After the eruption, survival and recruitment of growth form types varied significantly between habitats considered. The type and magnitude of vascular plant recovery in the first growing season following the eruption of Mount St. Helens appeared to depend upon the relationship between the nature of the disturbance which an area experiences, aspect, time of snowmelt and ongoing disturbances such as erosion.

Preadaptation to Fires and Snow

Periodic fires and climate (in particular heavy precipitation, much of it in the form of snow) may explain, in part, the high proportion of geophytes in the floristic composition of communities surrounding volcanoes of the Cascade Mountains. Similarly, the relatively frequent eruptions of Mount St. Helens (Mullineaux and Crandell 1981) may have a selective effect on vegetation structure that results in a higher proportion of plants with dormant primary meristematic tissue underground being found near Mount St. Helens. The chances for survival were found to be higher for plants buried by snow at the time of the eruption within the blast zone (Means *et al.* 1982, Adams and Adams 1982), but the reverse was found to be true in forests outside the blast zone where Antos and Zobel (1982) found reduced cover at sites with tephra on top of snow for shrubs, tree seedlings and erect evergreen herbs. Antos and Zobel, in commenting on the scarcity of *X. tenax* in habitats surrounding Mount St. Helens relative to its occurrence in similar habitats in other parts of the Cascades, note that timing of volcanic eruptions in relation to snow packs may greatly influence initial damage or survival of vegetation.

Montane forests and subalpine meadows of Washington do have recurrent fires and snowslides which remove above-ground plant biomass in a manner similar to that of the 18 May lateral blast of Mount St. Helens. Plants that regenerated in blowdown and scorched, dead forest habitats also regenerate after fires (Miller and Miller 1976, Agee and Scott 1983, Hitchcock and Cronquist 1981) and snowslides (Cushman 1981, Adams and Dale 1987). In the blowdown and scorched dead forests, most surviving plants regenerated from *in situ* buds of rhizomes, tubers, bulbs and corms. Antos and Zobel (1985a,b) found simliar results when investigating understory species covered by tephra from Mount St. Helens. In addition, these researchers noted that long-term survival was dependent upon reestablishment through the production of adventitious roots within the tephra, as well as surviving the burial. Species with the ability to regenerate from meristematic tissue located several cm below the surface have the greatest survival rate during fires (Flinn and Wein 1977, McLean 1969). Also, in blowdown and seared forest habitats some tall shrubs [*e.g.*, thimbleberry (*Rubus parviflorus*), salmonberry (*R. spectabilis*), and elderberry (*Sambucus racemosa*)] which had their above ground parts destroyed by the blast responded via adventitious buds forming epicormic shoots as they do following fires and snowslides. In this sense these species act as facultative geophytes.

Production of new foliage by plants with buds at the surface, small shrubs, and coniferous trees was restricted to areas protected by snow, north and northwest facing slopes, or to the scorched, dead forests in the case of hemicryptophytes and chamaephytes. Plants of the Pacific Northwest which possess buds 2.5 to 50 cm above ground level often have sclerophyllous evergreen leaves. The total loss of buds and leaves explains the scarcity of small shrubs in the devastation zone during the first growing season following the spring eruption. Both the proportion of chamaephyte species and their relative percent cover had decreased following the 18 May eruption. Many chamaephyte species [*e.g.*, Oregon grape (*Berberis nervosa*), salal (*Gaultheria shallon*) and twin flower (*Linnaea borealis*)] are residual components of burned areas in the Pacific Northwest and regenerate vegetatively within a year after a fire (Miller and Miller 1976). These species would be expected to be more abundant after the eruption. Adventitious buds can form on roots (especially injured roots), but this is least likely to happen during the spring (Hartmann and

Kester 1975). Dispersal of small shrubs back into the devastation zone should be relatively rapid in the Pacific Northwest because birds and mammals are major seed vectors for species possessing this growth form type (Best 1981).

Non-vascular plants that respond to fires were also the taxa that responded to the eruption of Mount St. Helens. For example, the most common moss found during our ongoing studies has been *Funaria hygrometrica,* a circumboreal species often found after forest fires and in campfire pits (Lawton 1971). Similarly, Discomycetes sporocarps (*e.g., Peziza violacea* and *Pyronema* spp.) were found throughout the devastation zone in 1980. These thermophilic fungi are often found after fires and in pasteurized soil used in greenhouses (Dennis 1978).

Preadaptation to Floods

At Mount St. Helens, some disturbances were similar to seasonal floods caused by heavy rains and snowmelt. On lower portions of the Toutle and Muddy Rivers, and Pine and Swift Creeks a slurry of mud, water and organic material washed down from the mountain sweeping away much of the vegetation. Marks on standing trees show the water levels were as much as 15 m above normal stream level as far as 33 km from the crater of Mount St. Helens. The largest flows occurred on the North Fork Toutle River where conifers and broad leaf deciduous trees were left standing but buried by meters of mud. Often standing trees had a ring of bark removed by the force of the flow leaving the cambial layer exposed.

Plant responses after mud flows are similar to methods of regeneration that these same species utilize following floods. Observations from the mud flows of Kautz Creek, Mount Rainier, Washington (Frehner 1957) and Mount Lassen, California (Beardsley and Cannon 1930) indicate that many trees died up to three years after being partially buried probably due to insufficient oxygen supply to their roots or from cambial damage. On the Kautz mud flow buried trees set seed the following spring and fall, and tree establishment was most abundant where snags provided protection against extreme temperatures and drought stress.

The difference in the growth form spectrum of mean percent cover for the mud flow habitat has broad implications for predicting the potential for vegetation recovery in this habitat type. *Populus trichocarpa* and *Salix* spp. partially covered by mud flows actually produced seed in 1980 after the eruption. Other species, including conifers, seeded in 1981. The short-term survival of trees on mud flows provided a seed source, and snags are more favorable habitat for germination and growth. As such, their short-term survival has a significant impact on future vegetation trends. Our results are slightly different than those of Halpern and Harmon (1983) who reported results for data collected in 1981 for the Muddy River mud flow which is closer to Mount St. Helens than our mud flow plots on the North Fork Toutle, and apparently had much fewer surviving tree snags in 1981 than we found in 1980. Our work is similar to that of Halpern and Harmon in that we too found regeneration from fragments to be present, and we found microsites within habitats to be diverse and to explain much of the diversity of the flora. Fragment regeneration appears to be more important on the North Fork Toutle mud flow than on the the Muddy River mud flow.

Potential for Fragment Regeneration as a Function of Habitat

Fragments were dispersed by the energy associated with lahars. Vegetative regeneration from transported fragments, such as that which might occur following a flood, occurs in mud flow and debris substrate. Regeneration from fragments has not been documented for volcanic eruptions. We found that mud flow and debris slide materials possess properties that enhance their potential as rooting media (Hartmann and Kester 1975, Adams and Dale 1987), such as: 1) neutral pH (6.7 ± 0.2, standard deviation); 2) low conductivity (less than two mmhos/cm); 3) sufficient aeration due to a predominance of sand; 4) moisture retention provided by silt and clay; 5) a small, but significant quantity of nitrogen; and, 6) emplacement temperature of deposits hot enough to kill root pathogens [*e.g.,* nematodes *Heterodera*) and water molds (*Rhizophotinia* and *Phythium*)], but not too hot to destroy beneficial bacteria (maximum temperature for debris and mud flow was 92°C) (Banks and Hoblitt 1981).

Plant fragments were also dispersed by the force of the blast itself. The capacity for the blast to disperse fragments is demonstrated by

eyewitness accounts of the eruption. For example, climbers at 2400 m on Mount Adams reported that plant fragments up to a meter in length and conifer cones landed around them shortly after 15:32 U.T. on 18 May 1980 (a minimum of one fragment/10m^2) (Jack Christiansen, pers. comm.). Fragments were found dispersed throughout the blowdown and seared forests, yet no fragments were found regenerating here. In this case, fragment regeneration might have been prevented by: 1) high temperatures that destroy meristematic tissue and beneficial symbionts; (blowdown and scorch emplacement temperatures ranged from 100 to 350°C) (Banks and Hoblitt 1981, Winner and Casadevall 1983); 2) coarser particle sizes that reduce moisture retentivity; and, 3) an almost impermeable cement-like layer with low porosity created when water combines with the fine-grained surface tephra layer that covers most of the potential regeneration sites in the blowdown and seared forests.

Vegetation Trends on the Debris Slide

The debris slide underwent a significant change in growth form spectra from 1980 to 1982 and showed seasonal variation in 1982. Although the proportion of annuals increases in temperate zones of the northern hemisphere following disturbances (Whittaker 1975), 60 percent for the July 1982 debris slide data is high. The reason for the abundance of annuals is believed to be due to the hot, dry conditions that exist on the surface of the debris slide. Other habitats in the northwest (e.g., serpentine outcrops and arid regions east of the Cascade Mountains) that support high proportions of annuals also have high temperature and low available water supplies. Alpine lupine (*Lupinus lepidus* var. *lobbii*), yellow monkey-flower (*Mimulus guttatus*) and miner's lettuce (*Montia sibirica*) which are often perennial, acted similar to many arid region species on the debris slide in that some individuals flowered and set seed the first year and then died, thus becoming annual. Temporary streams and pools common on the debris slide provide ephemeral resources similar to desert habitats. Annuals are able to exploit these temporary resources and then spend the more stressful periods as dormant seeds.

Overall, vegetation trends in our plots were not set back by the 19 March 1982 mud flow (Figure 2C-D). Nevertheless, this disturbance did vary in the magnitude of its impact on the debris slide, depositing more than 1 m of mud and pyroclastic material in some spots to lightly mantling other areas (Waitt *et al.* 1983). If localized disturbances such as this have high rates of occurrences on the debris slide, annuals such as wood groundsel (*Senecio sylvaticus*) and annual hairgrass (*Deschampsia danthonioides*) and geophytes adapted to chronic disturbances may remain dominant here. With more moderate disturbance rates, deciduous trees may become established and survive by producing adventitious roots, regenerating from fragments, and dispersing copious amounts of seeds.

The distance of seed sources from disturbance sites is critical to future vegetation trends, and is already a major factor in the Mount St. Helens area. For example, red alder (*Alnus rubra*) (a major component of flood plains of western Washington) did not survive in the blast zone. *Alnus rubra* performs well when started from seed on both mud and debris substrate (Adams *et al.* 1986), and this deciduous tree already has become dominant on lower reaches of the 1980 and 1982 mud flow deposits in the North Fork Toutle floodplain where seed sources are nearby. This same species is rare on the debris slide where seeds are less common. The rate at which *A. rubra* establishes may influence long-term successional trends. For instance, if the disturbances occur at even lower frequencies, then a mixed coniferous forest may have a chance to become established provided that *A. rubra* saplings do not become rapidly established and shade out conifer seedlings.

In our studies at Mount St. Helens we have been able to establish that plant growth form is important not only to initial recruitment onto newly deposited substrates of this stratolayer volcano, but in addition, is a significant factor in the composition and quantity of residual, surviving plant populations. Geophytes are not only the predominant survivors, but in addition, they are important in initial seedling recruitment from the blowdown above the Toutle River onto the debris slide.

Groups of species possess common adaptations (e.g., the position of dormant meristematic tissue) that influence survival. Initial prognosis of the Mount St. Helens impact areas underestimated the regenerative potential of the

vegetation and overestimated the success of aerial seeding with non-native grasses (Brown 1981, Carlson *et al.* 1982). If mechanisms of survival are understood and the composition of the preexisting flora is known, then more accurate predictions of species response and magnitude of vegetation recovery may be possible.

Acknowledgements

The authors thank D. Chapman, B. Hallet, E. Leopold, S. Malone, B. Meeuse, R. Paine and M. Slatkin for reading through initial drafts of this paper. We are especially appreciative of J. Franklin (U.S.D.A. Forest Service), D. Jamison, K. Russell and the Washington Department of Natural Resources for logistical support and suggestions. We thank J. Nishitani, R. Walker, D. Stuntz, S. Kaluzny, and J. Creager for technical assistance, the Earthwatch Volunteers, R. Holland and V. Daines for field assistance and S. Gessel for comments. This research was supported in part by the Center for Field Research (Boston, MA) and was seeded with NSF emergency funding (DEB-80-21460).

Literature Cited

Adams, V. D., and A. B. Adams. 1982. Initial recovery of the vegetation on Mount St. Helens. *In* S. A. C. Keller (ed.) Mount St. Helens: One Year Later, Eastern Washington University Press, Cheney. Pp. 105-113.

Adams, A. B., and V. H. Dale. 1987. Comparisons of Vegetative Succession Following Glacial and Volcanic Disturbances. *In* D. E. Bilderback (ed.) Mount St. Helens 1980: Botanical consequences of the Explosive Eruptions, University of California Press, Los Angeles. Pp. 70-147.

Adams, A. B., J. R. Wallace, J. W. Jones, and W. K. McElroy. 1986. Ecosystem resilience following the 1980 eruption of Mount St. Helens, Washington. *In* S. A. C. Keller (ed.) Mount St. Helens: 5 Years Later, Eastern Washington University Press, Cheney. In press.

Agee, J. K., and D. R. M. Scott. 1983. Ecological Effects of the Hoh Fire, Olympic National Park. Nat. Park Service Report #CX-9000-9-E079.

Antos, J. A., and D. B. Zobel. 1982. Snowpack modification of volanic tephra effects on forest understory plants near Mount St. Helens. Ecology 63: 1969-1972.

_____. 1985a. Plant form, developmental plasticity, and survival following burial by volcanic tephra. Can. J. Bot. 63:2083-2090.

_____. 1985b. Upward movement of underground plant parts into deposits of tephra from Mount St. Helens. Can. J. Bot. 63: 2091-2096.

_____. 1987. How plants survive burial: a review and initial responses to tephra from Mount St. Helens. *In* D. E. Bilderback (ed.) Mount St. Helens 1980: Botanical consequences of the Explosive Eruptions, University of California Press, Los Angeles. Pp. 246-261.

Banks, N. G., and R. R. Hoblitt. 1981. Summary of temperature studies of 1980 deposits. *In* P. W. Lipman and D. R. Mullineaux (eds.) The 1980 Eruptions of Mount St. Helens, Washington, U.S. Geol. Survey Prof. Paper #1250, U.S. Govt. Pr. Off. pp. 295-313.

Beardsley, G. F., and W. A. Cannon. 1930. Notes on the effect of a mud flow at Mount Shasta. Ecology 11:326-336.

Best, L. S. 1981. The Effect of Specific Fruit and Plant Characteristics on Seed Dispersal. University of Washington, Seattle. Ph.D. Dissertation.

Brown, L. A. 1981. SCS seeding evaluation on Mount St. Helens. U.S.D.A. Executive Summary. Available through U.S.D.A. Soil Conservation Service, Spokane, Washington 99201.

Carlson, J. R., J. R. Stroh, J. A. Oyler, and F. Reckendorf. 1982. Erosion control revegetation on land damaged by the 1980 Mt. St. Helens eruption. *In* R. L. Cuany and J. Etra (eds.) Proceedings: High-Altitude Revegetation Workshop No. 5, Colorado State University Water Resources Unit, Information Series No. 48, Ft. Collins, Colorado. Pp. 174-189.

Cushman, M. J. 1981. The Influence of Recurrent Snow Avalanches on Vegetation Patterns in the Washington Cascades. University of Washington, Seattle. Ph.D. Dissertation.

Dennis, R. G. W. 1978. Brish Ascomycetes. Second edition, Verlag Von J. Cramer, Germany.

Eggler, W. A. 1971. Quantitative studies of vegetation in sixteen young lava flows on the island of Hawaii. Trop. Ecol. 12:66-100.

Flinn, M. A., and R. W. Wein. 1977. Depth of underground plant organs and theoretical survival during fire. Can. J. Bot. 55:2550-2554.

Franklin, J. F., J. A. MacMahon, F. J. Swanson, and J. R. Sedell. 1985. Ecosystem responses to the eruption of Mount St. Helens. Nat. Geo. Res. 1:198-216.

Frehner, H. F. 1957. Development of Soil and Vegetation on Kautz Creek Flood Deposit in Mount Rainier National Park. University of Washington, Seattle. M.S. Thesis.

Griggs, R. F. 1933. The colonization of Katmai ash: a new and inorganic "soil." Amer. J. Bot. 21:265-277.

Halpern, C. B., and M. E. Harmon. 1983. Early plant succession of the Muddy River mudflow, Mount St. Helens, Washington. Amer. Midl. Nat. 110:97-106.

Hartmann, H. T., and D. E. Kester. 1975. Plant Propagation Principles and Practice. Third edition, Prentice Hall, Inc., Englewood Cliffs.

Hitchcock, C. L., and A. Cronquist. 1981. Vascular Plants of the Pacific Northwest. Fifth edition. University of Washington Press, Seattle.

Lawton, E. 1971. Moss Flora of the Pacific Northwest. Nichinan, Hattori Botanical Laboratory, Japan.

Lipman, P. W., and D. R. Mullineaux. 1981. The 1980 Eruptions of Mount St. Helens, Washington. U.S. Geol. Survey Prof. Paper #1250, U.S. Govt. Pr. Off.

Man'ko, Yu.I. 1974. The effect of contemporary volcanism on the vegetation of Kamchatkas and the Kurile Islands. In Komarov Lectures, Academy of Sciences (Vladivostok, Russia) 22:5-31.

McLean, A. 1969. Fire resistance of forest species as influenced by root systems. J. Range Manag. 22:120-122.

Means, J. E., W. A. McKee, W. H. Moir, and J. F. Franklin. 1982. Natural revegetation of the northeastern portion of the devastated area. *In* S. A. C. Keller (ed.) Mount St. Helens: One Year Later, Eastern Washington University Press, Cheney. Pp. 93-104.

Miller, M. M., and J. W. Miller. 1976. Succession after wildfire in the North Cascades National Park complex. Proceed. Ann. Tall Timbers Fire Ecol. Conf. 15:71-83.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley & Sons, New York.

Mullineaux, D. R., and D. R. Crandell. 1981. The eruptive history of Mount St. Helens. *In* P. W. Lipman and D. R. Mullineaux (eds.) The 1980 Eruptions of Mount St. Helens, Washington, U.S. Geol. Survey Prof. Paper #1250, U.S. Govt. Pr. Off. Pp. 3-15.

Raunkiaer, C. 1934. The Life Forms of Plants and Statistical Plant Geography: being the collected papers of C. Raunkiaer. Clarendon, Oxford, England (Transl. H. G. Carter, A. G. Tansley and M. Farrsbell).

St. John, H. 1976. The flora of Mount St. Helens, Washington. The Mountaineer 70:65-77.

Received 22 April 1986
Accepted for publication 24 February 1987

Sekiya, S., and Y. Kikuchi. 1889. The eruption of Bandaisan. Imperial University of Japan, College of Science Journal 3(2):91-172. Taken from Voight, B. H., H. Glicken, R. J. Janda, and P. M. Douglass. 1981. Catastrophic rockslide avalanche of May 18. *In* P. W. Lipman and D. R. Mullineaux (eds.) The 1980 Eruptions of Mount St. Helens, Washington, U.S. Geol. Survey Prof. Paper #1250, U.S. Govt. Pr. Off. Pp. 347-377.

Smathers, G. A., and D. Mueller-Dombois. 1974. Invasion and Recovery of Vegetation after Volcanic Eruption in Hawaii. Nat. Park Service, Sci. Mono. No. 5, Hawaii.

Swanson, D. A., T. J. Casadevall, D. Dzurisin, S. D. Malone, C. G. Newhall, and C. S. Weaver. 1983. Predicting eruptions at Mount St. Helens, June 1980 through December 1982. Science 221:1369-1376.

Tokarev, P. I. 1981. Volcanic Earthquakes of Kamchatka. Academy of Science (Vladivostok, Russia), (Transl. A. B. Adams, available at Suzzallo Library, University of Washington, Seattle).

Voight, B., H. Glicken, R. J. Janda, and P. M. Douglass. 1981. Catastrophic rockslide avalanche of May 18. *In* P. W. Lipman and D. R. Mullineaux (eds.) The 1980 Eruptions of Mount St. Helens, Washington, U.S. Geol. Survey Prof. Paper #1250, U.S. Govt. Pr. Off. Pp. 347-377.

Waitt, Jr., R. B., T. C. Pierson, N. S. MacLeod, R. J. Janda, B. Voight, and R. T. Holcomb. 1983. Eruption-triggered avalanche, flood, and lahar at Mount St. Helens—effects of winter snowpack. Science 221:1394-1397.

Weaver, C. S., J. E. Zollweg, and S. D. Malone. 1983. Deep earthquakes beneath Mount St. Helens: evidence for magmatic gas transport? Science 221:1391-1394.

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Mono. 30:279-338.

_____. 1975. Communities and Ecosystems. Second edition. MacMillan Pub. Co., Inc., New York.

Winer, B. J. 1971. Statistical Principles in Experimental Designs. Second edition, McGraw-Hill Book Co., New York.

Winner, W. E., and T. J. Casadevall. 1983. The effects of the Mount St. Helens eruption cloud on fir (*Abies* sp.) needle cuticles: analysis with scanning electron microscopy. Amer. J. Bot. 70:80-87.

Scott M. McCorquodale, Geosciences Department, Battelle, Pacific Northwest Laboratory
P.O. Box 999, Richland, Washington 99352

Fall-Winter Habitat Use by Elk in the Shrub-Steppe of Washington

Abstract

Fall-winter habitat use patterns of radio-collared Rocky Mountain elk (*Cervus elaphus nelsoni*) were studied on the Arid Lands Ecology Reserve in the shrub-steppe of Washington from October 1985 to March 1986. Collared elk showed activity-dependent habitat selection. *Artemisia tridentata/Poa sandbergii* areas were preferred by bedded (= resting or ruminating) elk while *Poa sandbergii* and *Bromus tectorum* areas without sagebrush were preferred for foraging. Foraging elk tended to use fewer vegetation types than bedded elk, indicating they were more selective of foraging habitats than bedding habitats. Grass biomass was about 2/3 less in *Poa* areas with sagebrush than in *Poa* areas without sagebrush. Foraging elk apparently selected areas without sagebrush because of the higher availability of forage relative to sagebrush-dominated areas. This study demonstrated the importance of considering animal activity in studies that seek to characterize habitat selection for a species.

Introduction

Information on habitat use patterns of elk is one of the most basic elements needed for informed habitat management. Ideally, these data should be collected over the range of habitats where elk occur. In recent years, data have been collected for elk inhabiting various forested areas (Marcum 1975, Irwin and Peek 1983, Jenkins and Starkey 1984). However, there is relatively little information on elk inhabiting non-forested environments.

In this paper, I report on fall-winter habitat use by Rocky Mountain elk inhabiting the shrub-steppe of south-central Washington. This information supplements the report of McCorquodale *et al.* (1986) which described spring-summer habitat use of elk in this same region.

Study Area

The study was conducted on the Arid Lands Ecology (ALE) Reserve, a 330-km² ecological reserve associated with the U.S. Department of Energy's Hanford Site in Benton County, Washington. This area is a treeless shrub-steppe region dominated vegetatively by big sagebrush (*Artemisia tridentata*) and bluebunch wheatgrass (*Agropyron spicatum*) (Daubenmire 1970). Vegetation associations dominated by big sagebrush and either Sandberg's bluegrass (*Poa sandbergii*) or cheatgrass (*Bromus tectorum*) are also present on the reserve. Periodic wildfires since 1950 have removed the sagebrush overstory from approximately 90 percent of the ALE Reserve. A more detailed description of the ALE Reserve has been provided by McCorquodale *et al.* (1986).

Winters are generally mild; however, the winter of 1985-86 was one of the most severe on record. A snowpack in excess of 10 cm covered the ground from late November to mid-January. Record cold temperatures and lengthy periods of fog were recorded throughout November and December.

Methods

Female elk were immobilized from a helicopter and were fitted with radio-collars, ear-tagged, and released. Collared elk were relocated approximately four times weekly by ground or aerial radio-tracking during daylight hours. Attempts were made to sample locations of both bedded and foraging elk. Attempts were also made to verify elk locations visually when this could be done without disturbing collared animals.

The availability of vegetation types was determined by randomly placing a dot grid over a map of the study area and systematically recording the vegetation type at each point (dot). This simulated sampling vegetation every 500 m throughout the study area and employed 1,209 sampled points.

Elk use of vegetation types was evaluated using the technique of Neu *et al.* (1974). Family-wise confidence intervals (C.I.) were calculated for the use of vegetation types (% of locations). This C.I. was compared to the availability of the types in the study area. If the calculated C.I. for use of a type did not include the availability of the type, use was considered statistically significant. A more detailed description of this technique has been provided by Byers *et al.* (1984.)

Data were analyzed by the following two-month divisions, which represented relatively distinct environmental periods: late fall = October and November, early winter = December and January, and late winter = February and March.

The biomass of grasses was estimated in representative stands of *Artemisia tridentata/Poa sandbergii* and *Poa sandbergii* and *Bromus tectorum* stands without sagebrush. A 40 m transect was established in each stand and 20 plots (20 cm x 50 cm) spaced at 2 m intervals, were hand-clipped. These samples were oven-dried at 40°C and weighed to the nearest gram.

Results

Four adult female elk were collared and relocated 379 times between October 1, 1985, and March 31, 1986. Over 95 percent of these locations were visually confirmed. The collared animals and their associates represented over 70 percent of the adult female elk on the ALE Reserve throughout the study period. Thus, the four collared elk were very representative of female elk on the reserve.

The *Artemisia/Poa* vegetation type was clearly preferred by elk for bedding throughout the study period, while *Poa* areas without a sagebrush overstory were preferred by foraging elk (Table 1). These previously burned *Poa* areas were also preferred by elk for bedding during February and March. *Agropyron-* dominated areas generally received little use during winter. Nearly all foraging activity was confined to areas without sagebrush. Previously burned areas with a cheatgrass understory were used heavily during December and January while snow remained on the ground. Riparian areas received little use except during late fall as foraging areas.

The biomass of grasses averaged 20.2 ± 1.5 g/m² (± 1 S.E.) in the *Artemisia/Poa* association, 63.5 ± 8.1 g/m² in the *Poa* association, and 232.7 ± 9.8 g/m² in the *Bromus* association.

Discussion

Radio-collared elk showed activity-dependent habitat selection patterns. Sagebrush areas offered vegetative cover preferred by bedded elk. The importance of cover for security and thermoregulatory advantages to elk has been shown previously (Beall 1976, Thomas *et al.* 1979). It should be noted that while statistical selection was shown for bedding in sagebrush types, 45-72 percent of bedded elk were located in areas without sagebrush (Table 1). Thus, elk showed a preference for bedding in sagebrush but were tolerant of varied vegetative conditions for bedding.

Elk were more selective of foraging habitats. No major foraging bouts were observed in sagebrush stands. Nearly all foraging occurred in *Poa* and *Bromus* stands without a sagebrush overstory. Both *Poa sandbergii* and *Bromus tectorum* are cool season grasses that showed a fall and late winter-early spring greenup. Selection for the *Poa* type was especially pronounced

TABLE 1. Selection of vegetation types by female elk on the Arid Lands Ecology Reserve, Washington

		% Elk Locations					
		Bedding			Feeding		
Vegetation Type	*% Area*	*Oct-Nov*	*Dec-Jan*	*Feb-Mar*	*Oct-Nov*	*Dec-Jan*	*Feb-Mar*
Burned *Artemisia/Agropyron*	49.0	20.7⁻	0.0⁻	11.1⁻	18.2.⁻	0.0⁻	8.0⁻
Burned *Artemisia/Poa*	15.8	24.5	27.6	61.1⁺	47.0⁺	38.8⁺	76.0⁺
Burned *Artemisia/Bromus*	24.1	11.3⁻	17.2	0.0⁻	25.8	61.2⁺	0.0⁻
Riparian	0.1	0.0	0.0	0.0	9.1	0.0	0.0
Artemisia/Agropyron	2.9	7.5	0.0	0.0	0.0	0.0	0.0
Artemisia/Poa	2.4	20.7⁺	41.4⁺	27.8⁺	0.0	0.0	16.0
Artemisia/Bromus	5.8	15.1	13.8	0.0	0.0⁻	0.0⁻	0.0
Number of Locations		53	58	54	66	98	50

+ denotes usage greater than availability, $P < 0.05$
− denotes usage less than availability, $P < 0.05$

during February and March when snow had melted and new growth was abundant.

Elk showed a strong preference for the *Bromus* type during December and January when snow covered the ground. Elk were rarely observed pawing through the snow to reach buried grass but appeared to be heavily using tall forbs and grasses such as prickly lettuce (*Lactuca serriola*), marsh-elder (*Iva xanthifolia*), and Great Basin wildrye (*Elymus cinereus*).

Differences in forage biomass were noted between areas with and without sagebrush, and elk apparently foraged in areas without sagebrush because of the higher biomass available there.

This study demonstrates the importance of considering the effect of activity on habitat selection patterns. if habitat-use data are biased toward certain activities or if activity-dependent preferences are obscured by failing to properly stratify relocation data, results may be suspect and habitat managers may fail to provide habitat for all the daily needs of elk or other wildlife species.

Acknowledgments

I would like to thank W. H. Rickard of the Pacific Northwest Laboratory for his assistance and support. I also thank K. Pedevillano for assistance in the field. This work was supported by the U.S. Department of Energy under Contract DE-AC06-76RLO 1830.

Literature Cited

Beall, R. C. 1976. Elk habitat selection in relation to thermal radiation. *In* S. R. Hieb (ed.) Proc. Elk-logging-roads symp., University of Idaho, Moscow. Pp. 97-100.

Byers, C. R., R. K. Steinhorst, and P. R. Krausman. 1984. Clarification of a technique for analysis of utilization-availability data. J. Wildl. Manage. 48:1050-1053.

Daubenmire, R. 1970. Steppe vegetation of Washington. Wash. Agric. Exp. Stn. Tech. Bull. 62, Washington State University.

Irwin, L. L., and J. M. Peek. 1983. Elk habitat use relative to forest succession in Idaho. J. Wildl. Manage. 47:664-672.

Jenkins, K. L., and E. E. Starkey. 1984. Habitat use by Roosevelt elk in unmanaged forests of the Hoh Valley, Washington. J. Wildl. Manage. 48:642-646.

Marcum, C. L. 1975. Summer-fall habitat selection and use by a western Montana elk herd. University of Montana, Missoula. Ph.D. Dissertation.

McCorquodale, S. M., K. J. Raedeke, and R .D. Taber. 1986. Elk habitat use patterns in the shrub-steppe of Washington. J. Wildl. Manage. 50:664-669.

Neu, C. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. J. Wildl. Manage. 38:541-545.

Thomas, J. W., H. Black, Jr., R. J. Scherzinger, and R. J. Pederson. 1979. Deer and elk. *In* J. W. Thomas (ed.). Wildlife habitats in managed forests—the Blue Mountains of Oregon and Washington. U.S.D.A. Handbook No. 533. Washington, D.C. Pp. 104-127.

Received 20 June 1986
Accepted for publication 19 March 1987

R. Scott Lutz and **John A. Crawford,** Dept. of Fisheries and Wildlife
Oregon State University, Corvallis, Oregon 97331

Seasonal Use of Roost Sites by Merriam's Wild Turkey Hens and Hen-Poult Flocks in Oregon

Abstract

Characteristics of trees and cover types in which Merriam's wild turkeys (*Meleagris gallopavo merriami*) roosted were described for 36 roosts used by hens during winter, spring, and summer in north-central Oregon from 1981 to 1982. Four of 14 cover types were used for roosting; only mature mixed conifer was used significantly more than it occurred on the study area. Number of roost trees/site, canopy cover, slope, and DBH (diameter of tree at breast height) were roost characteristics that differed among seasons. Ponderosa pines (*Pinus ponderosa*) ($\bar{x}$ DBH = 67.8 cm) were used for roosting most frequently in winter and spring, whereas smaller ($\bar{x}$ DBH = 47.7 cm) Douglas-firs (*Pseudotsuga menziesii*) were used most often in summer. Average number of trees/site ranged from three in spring to six in winter. Roosts were located more frequently on steep slopes during winter, likely an outcome of the restricted distribution of mature mixed conifer cover type in winter habitat. In summary, although hen poult flocks roosted in the same cover type during winter, spring, and summer, seasonal differences in roost characteristics were attributed to flock size and composition.

Introduction

Roost sites of Merriam's wild turkeys have been described for several locations within the original range of this subspecies. Ponderosa pine trees were most commonly reported as roosting habitat in Colorado (Hoffman 1968) and Arizona (Boeker and Scott 1969), but Douglas-fir and white fir (*Abies concolor*) in mixed-conifer stands were used by turkeys in New Mexico (Jones 1981). Large, mature trees were used most often for roosting in these areas. Merriam's wild turkeys have been introduced into several western states; however, little research has been conducted on cover types or trees used by turkeys for roosting in these areas. Mackey (1984) found that Douglas-fir cover type (10 of 17) and trees were used most commonly for roosting from February through August in Washington, and Jonas (1966) reported the ponderosa pine community was most frequently used for roosting habitat in Montana.

Previous research focused most often on the tree or trees used for roosting; little work has been reported on cover types in which roost trees were located. In addition, generally only one tree measurement (DBH) was taken, no information was collected on the age and sex of birds using roosts, and most research described roosts from only one season or combined seasons.

The purpose of this project was to better understand roosting habitat used by adult hen and hen/poult groups of Merriam's wild turkeys in Oregon, where the birds were introduced in 1961 (Mace 1965). Our objectives were to describe cover types used for roosting, to describe characteristics of trees selected for roosting within cover types, and to test for differences in seasonal use of roost sites. Adult hens were selected for study because adults, although they composed only 28 percent of the female segment of the sample in our study, contributed 91 percent of the broods (Crawford and Lutz 1984). Information about these cover types and roost tree characteristics may be useful to landmanagers interested in managing areas for Merriam's wild turkeys.

Materials and Methods

Twelve adult hens, two in 1981 and 10 in 1982, were trapped from January to April and equipped with radio transmitters (Telonics Inc., Mesa, Arizona) on the White River Game Management Area, Mount Hood National Forest, and adjacent private lands in southern Wasco County, Oregon. Nine of the 12 hens successfully produced broods. We attempted to find roosts twice monthly by selecting one radio-equipped hen and determining the roost location one hour after sunset. We selected a different hen during each roost finding attempt to insure that all hens contributed to roost locations. Cover types on the 135,141-ha study area were mapped from LANDSAT satellite imagery (Murray 1981). Study

area boundaries were based on total annual locations because of considerable overlap of areas used by radio-marked hens throughout the year. Physiographic (percent slope, distance to nearest ridge, and aspect) and vegetative characteristics were used to describe roost sites. Measurements of individual roost trees included diameter at 1.4 m (DBH), percent canopy closure, canopy height, and height to lowest living and dead limbs. Percent slope and all height measurements were estimated with a clinometer. Percent canopy closure was estimated with a sighting tube (James and Shugart 1971) at four randomly selected points within 3 m of roost trees. Presence of stumps within the roost site was used as evidence of logging activity. Percentages of forested and non-forested cover types within 0.33 km of the roost site were determined from aerial photos with a grid of 50 randomly distributed points (Marcum and Loftsgaarden 1980). This area around the roost was within the daily movement range of hen-poult flocks (Crawford and Lutz 1984). Numbers of droppings at bases of trees were used to classify amount of use (light = < 10 droppings, moderate = 10-50 droppings, heavy = > 50 droppings. Seasons of use were winter (16 November-28 February), Spring (1 March-31 May), summer (1 June-15 September), and fall (16 September-15 November).

Chi-square for goodness of fit (Sokal and Rohlf 1969,552) were used to test for differences between expected and observed numbers of roosts in all cover types. If a difference was detected, confidence interval estimates (Neu *et al.* 1974, Byers *et al.* 1984) were calculated for each cover type to identify cover types that contributed to the difference. One-way analysis of variance (Nie *et al.* 1975,422-433) was used to test for differences in physiographic and vegetative characteristics of roosts among seasons. If there were differences in characteristics and the assumption of homogeneity of variance was met, Student-Neuman-Keuls multiple comparison tests (Nie *et al.* 1975,428) with harmonic means (Hull and Nie 1981,307) were used to identify which seasons differed. The 95 percent confidence level was accepted as significant.

Results and Discussion

A total of 39 roost sites was found. Twelve roost sites from each of three seasons (winter, spring, and summer) were analyzed for seasonal differences. Fall was not included in the analyses because only one roost was located. Fall roosts were difficult to locate because of frequent, long movements by hens during that season. Two roosts were used during more than one season (spring and fall) and were excluded from the seasonal analysis.

The sex and age composition of groups at roosts differed among seasons. Spring roosts were used exclusively by adult hens. Adult hens and poults occupied summer and fall roosts. In winter, roosts were used by adult hens and yearlings of both sexes.

Cover Type Use

Fourteen cover types were classified. Eleven of the cover types on the study area were forested (Table 1). Nonforested habitats (range, irrigated lands, grain) occupied less than six percent of the study area.

Four of the 11 forested cover types on the study area were used for roosting. Mature mixed conifer was selected for roosting in all seasons (92%-winter,75%-spring,59%-summer) and was the only cover type used significantly more than it occurred on the study area (Table 1). Ponderosa pine, ponderosa pine/Douglas-fir/oak (*Quercus garryana*), and ponderosa pine/white oak cover types also were used for roosting.

Cover adjacent to roost sites was primarily (x = 80%,range = 58-96) forested (Table 2). Scott and Boeker (1977) found that adjacent forest cover affected use of roost sites and suggested a maximum distance of 90 m between roost sites and forested cover. Low elevation sites (< 1000 m) on our study area have an 80-year history of small-scale, selective logging activity (Williams 1978,13); however, only 7.5 percent of the roost sites had been logged, in contrast with data from New Mexico (Jones 1981) where 46 percent of the roost sites had been logged. These contrasting results indicated a rather broad range of response by Merriam's wild turkeys to logging near roost sites.

Roost Tree Characteristics

Within the mature mixed-conifer cover type, hen-poult flocks used large (DBH = 59.3 cm), dominant trees most frequently for roosting. Increment borings indicated that trees of this diameter

TABLE 1. Descriptions of forested cover types, percentage of study area occupied by each cover type, and percentage of roosts (N = 36) in the cover types used by Merriam's wild turkeys in southern Wasco Co., Oregon, 1981-1982.

Cover type	*Cover type description*	*% available*	*% of roosts*
Oregon White Oak	Found at low elevations (660-750 m) on the eastern edge of the study area. Oak was the dominant species in the shrub, understory, and overstory strata.	24.6	0
Ponderosa pine	Found primarily on the southern portion of the study area on the WSIR between 600 and 1000 m. Both overstory and understory consisted of ponderosa pine.	17.8	2.7
Mature mixed conifer	At elevations below 750 m these stands were restricted to steep north facing slopes. At these elevations, the overstory was composed of Douglas-fir and ponderosa pine. At elevations above 750 m, the overstory was true fir and Douglas-fir.	14.2	75.0[a]
Ponderosa pine/Douglas-fir/ white oak	Found as a transition between ponderosa pine/oak and the mixed conifer stands between 750 and 825 m. Generally there was a widely dispersed overstory with a dense understory of ponderosa pine, Douglas-fir, and oak.	12.5	11.1
Ponderosa pine/white oak	Also found at the eastern edge of the study area; often adjacent to oak stands. The overstory consisted of ponderosa pine and oak was consistently found in the understory.	9.5	11.5
Thinned mixed conifer	Single-story stands with a Douglas-fir or ponderosa pine overstory. These stands occurred from 700-900 m and had been thinned during the past 15 years.	7.8	0
Young mixed conifer	Often due to selective logging that had removed overstory species. The result was a mixture of dense sapling to pole size (Douglas-fir, True fir) stands interspersed with small open areas often seeded to orchardgrass (*Dactylis glomerata*).	7.7	0
Old clearcuts	These habitats ranged in size from 5 to 75 ha and were the result of logging 10-20 years ago. Habitats consisted of either single-story conifer plantations or dense, multi-layered shrub communities.	0.6	0
Mixed deciduous	These stands were most often in riparian zones and consisted of dense shrub patches interspersed with small, wet meadows.	0.1	0
Recent clearcuts	Found primarily in the mixed conifer stands above 750 m. These habitats were logged within the past 5 years and ranged in size from 5 to 15 ha.	0.1	0
Shelterwoods	Generally located at the upper elevations (>900 m) in mixed conifer stands. The stands consisted of widely dispersed overstory of mature Douglas-fir or true fir and a well-developed mixed conifer understory.	0.1	0
Other	Grain fields, rangeland, and irrigated pastures	5.5	0

[a]Use of cover types significantly greater than expected ($P < 0.05$).

were >300 years old. Merriam's turkeys roosted exclusively in either ponderosa pine (62.3%) or Douglas-fir (37.7%) trees.

DBH of roost trees in Oregon (59.3 cm) was among the highest reported. Mean DBH in other areas ranged from 45 cm in Montana (Jonas 1966) and New Mexico (Jones 1981) to 64.5 cm in Arizona (Boeker and Scott 1969). Differences in sizes of trees used for roosting may be a function of sizes available, but neither we nor these authors determined DBH of trees not used for roosting by turkeys. Although these results indicated regional differences in sizes of trees used for roosting, all roosts typically were composed of large, mature trees in each of the areas.

Seasonal Differences

Very few traditionally used roost sites were identified; only two sites were used during more than one season and 82 percent of all sites were lightly used. All sites used in spring were used lightly, whereas 79 percent of winter and 67 percent of summer roost sites were used lightly. In contrast, Jones (1981) found that all (N = 17) winter roost sites were repeatedly used (i.e., at least moderate use), but only one of 22 summer roost sites was used more than once.

Number of roost trees/site ($F = 11.9, P < 0.001$), DBH ($F = 7.4, P < 0.001$), canopy cover ($F = 11.9, P < 0.001$), and slope ($F = 7.6, P < 0.001$) differed among the three seasons (Table 2). An average of 2.9 (1-10) trees composed spring roosts, whereas winter and summer roost sites consisted of 5.4 (1-9) and 5.9 (1-10) trees, respectively. Roosts were in multi-layered, mature, mixed-conifer cover types. Number of trees used during the seasons was probably related to turkey flock size. Spring flocks often were composed of <5 individuals and summer and winter flocks of >30 individuals. There was a similar trend among roost sites in ponderosa pine in Colorado, although they were larger and averaged 17 trees/site in winter and six trees/site for spring and summer combined (Hoffman 1968). Jones (1981), in New Mexico, found eight trees/site in winter and two trees/site in summer.

DBH of summer roost trees was smaller than the DBH of winter and spring trees. Summer roost sites often were located in sawlog sized trees (Baker 1950) in the mature mixed conifer cover type. Once poults were capable of flying, they used low tree limbs to move into the tree canopy. Often sawlog sized trees offered branch structure of this type. Branch structure provided by Douglas-fir and Ponderosa pine of this size was likely an important characteristic of roosts used by hens with young poults in summer.

TABLE 2. Characteristics of roost cover types and trees used by Merriam's wild turkey during three seasons in southern Wasco County, Oregon, 1981-1982.

Characteristics	*Mean (Standard Error)*		
	Winter (N = 12)	*Spring (N = 12)*	*Summer (N = 12)*
Cover type			
Trees/site (#)[a]	5.4(0.4)	2.9(0.3)	5.7(0.5)
Forested habitat (%)	76.4(6.4)	87.4(2.2)	77.6(4.7)
Ponderosa pine (%)	52.0	76.0	64.0
Distance to ridge (m)	57.3(5.8)	37.0(4.9)	51.8(4.6)
Tree			
DBH (cm)[a]	63.9(3.1)	71.7(4.3)	47.7(2.1)
Canopy[a] coverage (%)	20.7(2.6)	19.1(3.4)	42.6(5.0)
Slope (%)	24.2(2.6)	16.2(3.2)	12.0(1.5)
Height to 1st living limb (m)	9.8(0.8)	10.3(0.9)	9.7(0.9)
Height to 1st dead limb (m)	5.2(0.7)	5.4(1.4)	4.2(0.9)
Crown height (m)	17.2(1.3)	18.5(1.2)	15.2(0.9)

[a]Significantly different among seasons ($P < 0.05$)

Canopy cover of winter and spring roosts was similar and averaged 20 percent, whereas summer roosts averaged 43 percent. High canopy cover reflected the increased use of smaller sized trees as roost trees during summer. Mackey (1984) reported mean canopy cover of 73.5 percent (all seasons combined) at roosts in Washington. The high canopy cover from Mackey's study likely was related to use of Douglas-fir trees for roosting by turkeys. Mackey proposed that canopy cover may be important for thermal regulation in winter by roosting birds.

Slope at spring and summer roosts was less than at winter roosts. In addition, winter roost sites were found almost exclusively (93%) on north-facing slopes. During other seasons, all aspects were used. Steep, north-facing slopes at winter roosts probably reflected the restricted distribution of mature mixed conifer stands at

lower elevations where turkeys were most commonly found during winter. Most mature conifer stands in less rugged terrain at these elevations had been logged within the last 80 years.

Among seasons, mature mixed conifer was the only cover type used selectively for roosting. Although the same cover type was used during the three seasons, species and sizes of trees used for roosting differed seasonally. These differences appeared related to the ages of birds using the roost. For example, adult and yearling birds used larger ponderosa pine and Douglas-fir trees during winter and spring than adults with poults used during summer.

Literature Cited

Baker, F. S. 1950. Principles of silviculture. McGraw-Hill Book Co. New York.

Boeker, E. L., and V. E. Scott. 1969. Roost tree characteristics for Merriam's turkey. J. Wildl. Manage. 33:121-124.

Byers, C. R., R. K. Steinhorst, and P. R. Krausman. 1984. Clarification of a technique for analysis of utilization-availability data. J. Wildl. Manage. 48:1050-1053.

Crawford, J. A., and R. S. Lutz. 1984. Merriam's wild turkey habitat use and movements. Oregon Dept. Fish and Wildl. Final Rep. PR-W-79-R-2.

Hoffman, D. M. 1968. Roosting sites and habits of Merriam's turkeys in Colorado. J. Wildl. Manage. 32:859-866.

Hull, C. H., and N. H. Nie. 1981. SPSS Update 7-9. McGraw-Hill Book Co., New York.

James, F. C., and H. H. Shugart, Jr. 1971. A quantitative method of habitat description. Audubon Field Notes. 24:727-736.

Jonas, R. J. 1966. Merriam's turkeys in southeastern Montana. Mont. Fish and Game Dept. Tech. Bull. 3.

Jones, K. H. 1981. Effects of grazing and timber management on Merriam's turkey habitat in mixed conifer vegetation of southcentral New Mexico. New Mexico State Univ., Las Cruces. M.S. Thesis.

Mace, R. U. 1965. Turkey talk. Oregon State Game Comm. Bull. 5:3-6.

Received 19 December 1986
Accepted for publication 23 March 1987

Acknowledgments

We thank R. Anthony and W. Krueger for reviewing the manuscript. This work was supported by funding from Oregon Department of Fish and Wildlife (ODFW) (PR-W-79-R-2) and Mount Hood National Forest (MHNF). We thank R. Denney, ODFW, D. Longrie, MHNF, and T. Luther (Warm Springs Indian Reservation) for their cooperation. C. Heath aided in collection of roost site data. This is Technical Publication 7828 of the Oregon Agricultural Experiment Station.

Mackey, D. L. 1984. Roosting habitat of Merriam's turkeys in south-central Washington. J. Wildl. Manage. 48:1377-1382.

Marcum, C. L., and D. O. Loftsgaarden. 1980. A nonmapping technique for studying habitat preference. J. Wildl. Manage. 44:963-968.

Murray, R. J. 1981. Landsat-based vegetation and landuse inventory for five Columbia Basin Counties in Oregon. Environmental Remote Sensing Applications Lab., Oregon State Univ.

Neu, C. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. J. Wildl. Manage. 38:541-545.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. SPSS: Statistical package for the social sciences. 2nd edition. McGraw-Hill Book Co., New York.

Scott, V. E., and E. L. Boeker. 1977. Responses of Merriam's turkey to pinyon-juniper control. J. Range Manage. 30:220-223.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Co., California.

Williams, C. K. 1978. Vegetation classification for the Badger allotment, Mt. Hood National Forest. Oregon State Univ. Corvallis. Ph.D. Dissertation.

George W. Cox and **Douglas W. Allen,** Department of Biology
San Diego State University, San Diego, CA 92182-0057

Sorted Stone Nets and Circles of the Columbia Plateau: A Hypothesis

Abstract

On level to gently sloping surfaces of the Columbia Plateau, circles and networks of size-sorted stones are frequently found associated with large earth (Mima) mounds. These distinctive beds of stones have been regarded as either the product of periglacial freeze-thaw processes or of erosion. We examined circular stone beds around mounds of different size and mapped the relation of stone nets to mounds and recent pocket gopher activity areas. Our study plots were adjacent to the Lawrence Memorial Grassland Preserve, near Shaniko, southern Wasco County, Oregon. The degree of completeness of stone circles was directly correlated with mound diameter and height. Pocket gophers tunneled extensively in intermound areas with well-developed stone nets. Several species of fleshy-rooted perennial plants are largely confined to the stone net microhabitat, probably by more intense pocket gopher feeding elsewhere. The beds of sorted stones appear to be formed and maintained by the mining of the underlying soil by pocket gophers that dig foraging tunnels into rocky intermound areas in search of food plants. These observations suggest that pocket gophers are much more important in landscape and vegetational dynamics than previously recognized.

Introduction

Large areas of the Columbia Plateau are covered by earth mounds, known as Mima mounds, that are commonly 0.5-1.0 m in height and 15-25 m in diameter. A distinctive feature of much of this landscape is the presence of sharply defined beds of bare, sorted stones that partially or completely encircle the mounds and occasionally form intermound stripes and polygonal networks. Well developed stone circles and nets of this type have been reported from eastern Washington (Kaatz 1959, Tallyn 1980), southwestern Idaho (Malde 1961, 1964, Fosberg 1965), and north-central Oregon (Waters and Flagler 1929, Nelson 1977, Johnson 1982). Mounds surrounded by well developed stone circles also occur in Siskiyou and Shasta Counties, California (Masson 1949).

Kaatz (1959), Malde (1961, 1964), and Fosberg (1965) state that the beds consist of tightly packed stones ranging in size from pebbles to boulders. The stones are sorted by size, with larger elements predominating on top. Frost-shattered stones are common in the beds, and tabular stones are sometimes found packed on edge into the rock network, their long axis reportedly lying parallel to the border of narrow beds, or showing a random orientation in wider areas. The zone of soil-free stones tends to be less than 30 cm thick, and may rest directly on basaltic bedrock or overlie stony soil of variable depth. These beds are sometimes termed "gutters" by proponents of geological hypotheses of their origin (Goldthwait 1976).

Circular and polygonal nets are restricted to surfaces less than about two percent in slope (Malde 1964). As slope increases the beds transform into intermound stripes corresponding to drainageways, and these increasingly become oriented parallel to the slope, separating "beaded" lines of interconnected mounds (Malde 1961, 1964). Sorted stone stripes not associated with mounds, which may represent a different phenomenon, also occur on steep slopes of the Columbia Plateau (Pyrch 1973).

Two major hypotheses have been offered for the origin of these systems of mounds and stone networks: differential erosion and periglacial freeze-thaw dynamics. Waters and Flagler (1929) concluded that the mounds were the result of erosion of volcanic ash deposited over the surface of the basaltic rock, with the intermound zones being "erosion furrows" and the bare rock beds more heavily eroded "erosion channels." This view was supported by Knechtel (1952) and Washburn (1980). Kaatz (1959), Brunnschweiler (1962), Malde (1961, 1964), and Fosberg (1965) considered the mounds and sorted stone nets to be a consequence of periglacial processes. Kaatz (1959) postulated that the mounds were the remnant centers of ice-wedge polygons which suffered erosion when the climate warmed and the ice wedges melted. He considered the stone nets

and stripes to have formed by frost-sorting action after the mounds had been defined. Brunnschweiler (1962) and Malde (1961, 1964) concluded that the mounds and stone networks formed simultaneously in the late Pleistocene due to processes of freeze-thaw and solifluction. Kaatz (1959) stated that the stone networks "defy any possible alternative to frost action for their formation" and Malde (1964) that they "are reasonably interpreted only by frost action." Fosberg (1965) inferred that the stone networks were the results of intense frost sorting, and may have formed prior to deposition of the soil material that was later eroded to form the mounds. More recent studies on the Deschutes-Umatilla Plateau of north-central Oregon (Nelson 1977, Johnson 1982) have tended to support the hypothesis of frost-sorting by showing that small-scale frost action still occurs.

In contrast, several recent studies (Cox 1984, Cox and Gakahu 1986, Cox and Allen 1987) have provided support for the hypothesis that North American Mima mounds are formed by soil translocation by pocket gophers. Past statements of this hypothesis have not accounted for the strikingly developed stone circles and nets of the Columbia Plateau, other than to suggest that large rocks are often exposed in intermound areas as a result of mining and removal of the soil by pocket gopher tunneling (e.g., Dalquest and Scheffer 1942, Scheffer 1947). We therefore investigated a typical mound and stone net site on the Columbia Plateau in north-central Oregon to determine if the stone nets 1) are so intimately associated with mounds as to demand a common mechanism of origin, and 2) if soil mining and translocation by pocket gophers can account for formation of sorted stone circles and nets.

Methods

Studies were carried out at the Lawrence Memorial Grassland Preserve, a 153-ha area near Shaniko, Wasco County, Oregon (44°57'N, 120°48'W), and on adjacent rangeland of the Priday Brothers Corporation. The preserve, a Registered National Natural Landmark owned by the Nature Conservancy, includes a portion of the Shaniko Plateau, formed of Columbia River Basalts, together with several ravines that slope steeply northward into the canyon of Ward Creek, 122 m below. The site has a cold semi-desert climate, with an average annual rainfall of 280 mm. The surface of the plateau is typically mounded "biscuit scabland," with numerous Mima mounds up to about 1 m in height and 20 m in diameter. The mound soils are classed as Condon aeolian silt loams, and the soils of intermounds as Bakeoven residual very cobbly loams. The vegetation of the mounds and deeper upland soils is dominated by Idaho fescue (*Festuca idahoensis*) and bluebunch wheatgrass (*Agropyron spicatum*), while the shallow intermound soils are dominated by scabland sagebrush (*Artemisia rigida*), Sandberg bluegrass (*Poa sandbergii*), seven taxa of biscuitroot (*Lomatium* spp.), and bitterroot (*Lewisia rediviva*). The northern pocket gopher (*Thomomys talpoides*) is abundant. A detailed physical and biotic inventory of the Preserve is given by Copeland (1980).

Our studies were conducted between 24 and 28 May 1986. Data were collected on two study plots. We measured and mapped mounds on a 90 x 150 m plot (1.35 ha) located on a level area of the plateau surface, using a surveying level. The degree of development of stone circles around all mounds on this plot was recorded. A second plot, 40 x 70 m in size (0.28 ha), was centered on a level intermound area about 20 x 50 m in extent, surrounded by eight well-developed mounds. This extensive intermound area exhibited a scattering of soil islands within a complex network of stone circles and polygons (Figure 1). We subdivided this plot with a 10 x 10 m grid and sketch-mapped the mounds, soil islands, and sorted stone networks, together with the locations of recent (to about 2 yr of age) pocket gopher heaps located in proximity to stone beds or within islands of soil and rock surrounded by stone polygons. Additional observations were made on the relationship of surficial evidence of pocket gopher activity to mounds and sorted stone beds at several other locations on the plateau top and on ravine slopes.

Plant names are based on Hitchcock and Cronquist (1973) and statistical procedures on Zar (1974).

Results

A close association existed between mounds and stone circles. A few mounds were completely encircled by stone beds, although on our 1.35-ha plot stone circles ranged from 0 percent to 85

Figure 1. Sorted stone nets enclosing islands of soil and rock in a level intermound site adjacent to the Lawrence Memorial Grassland Preserve near Shaniko, southern Wasco County, Oregon.

percent in completeness (n = 37). A significant relationship existed between the size of the mound and the degree of development of the encircling stone bed. Percent completeness was highly correlated with mound height ($r = 0.479$, $P < 0.01$) and volume ($r = 0.472$, $P < 0.01$), and significantly correlated with mound diameter ($r = 0.348$, $P < 0.05$).

Where present, stone circles usually lay within 1 m of the base of the mound slope. On very slight slopes (< 2-3°), the stone beds were usually best developed on the downslope sides of mounds. For some of these mounds the stone beds on the downslope side appeared to bulge above the general level of the immediately adjacent intermound zone. On steeper slopes, stone beds sometimes closely encircled the upper and lateral sides of mounds, but diverged to create stripes extending downslope for a short distance (Figure 2A).

The stone beds typically showed a sharp boundary with both mound and intermound soils. The larger rocks of the central areas of the beds were densely encrusted with the black lichen *Lecidea cascadensis* (Rossman 1977) on their exposed surfaces, indicating long-term stability. In many locations, both on mound and intermound edges of stone nets, small pebbles and stones without strongly developed black lichen cover predominated. We did not observe unusual patterns of vertical packing or orientation of tabular rocks in these networks.

The mapped 0.28-ha plot exhibited stone beds that bounded or partially encircled the adjacent mounds, together with an extensive intermound network containing irregularly shaped islands of soil and rock ranging in area from about 1 m^2 to over 100 m^2 (Figure 3). The islands contained large stones, and appeared to differ from the surrounding stone beds only in the presence of finer textural material between and partially covering the larger stones.

Recent pocket gopher heaps were present throughout the intermound complex of stone nets and soil-and-rock islands. These heaps (n = 56) were concentrated at the edges of the stone beds (34), although many lay in the interior of the soil-and-rock islands (19). Three heaps, however, lay on the surface of stone beds. Numerous unmapped heaps were also present on the surfaces of

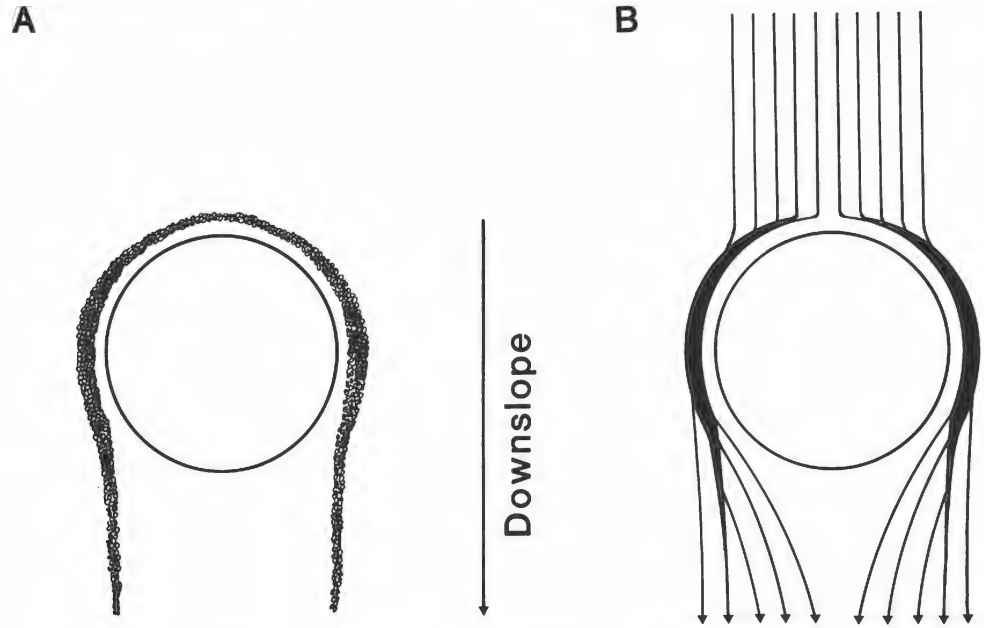

Figure 2. A. Arrangement of sorted stone beds bordering a Mima mound on a slope of 3-5° at the Lawrence Memorial Grassland Preserve, southern Wasco County, Oregon. B. Pattern of water movement and concentration in relation to the mound and stone net pattern shown in A.

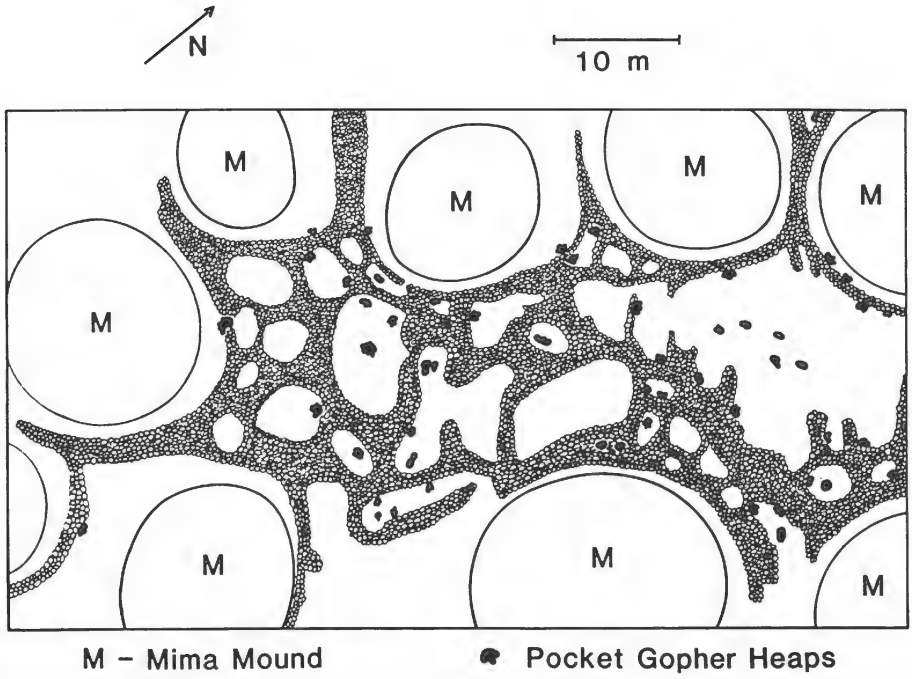

Figure 3. Pattern of Mima mounds, stone circles, intermound stone nets and islands of soil and rock on a 40 x 70 m plot centered on a large intermound flat on land adjacent to the Lawrence Memorial Grassland Preserve, southern Wasco County, Oregon. Pocket gopher heaps are shown only within and adjacent to the network of stone beds; heaps were also abundant on the mound surfaces.

the adjacent mounds. The pocket gopher heaps consisted of fine soil, gravel, and pebbles up to a maximum diameter of about 60 mm.

Discussion

The close proximity of sorted stone circles to edges of mounds and the significant relationship of stone circle development to mound size suggest that the mounds and sorted stone circles form concurrently, contrary to the suggestions of Kaatz (1959) and Fosberg (1965). Moreover, the presence of small, lightly weathered, lichen-free stones at the edges of some beds suggests that pavement formation is still occurring, or that, at least, these systems are to some degree dynamic.

We postulate that tunneling and the translocation of soil by geomyid pocket gophers, in addition to forming the mounds, create and maintain the sorted stone circles and nets that exist in association with these mounds on the Columbia Plateau. This hypothesis is outlined in detail below, and although we have formulated it specifically for the conditions prevailing at the Lawrence Memorial Grassland Preserve, we propose that it applies in principle to other Columbia Plateau localities.

Pocket gophers maintain their permanent nest and food storage chambers in the mounds because of frozen or waterlogged conditions of intermound areas during late winter and early spring. They tunnel extensively into the intermound zone during dry seasons. This tunneling is evidenced by the deposition of heaps on the intermound margins of stone networks and on islands of soil and rock enclosed by stone nets. The distribution of heaps also demonstrates that the animals commonly tunnel beneath the stone beds. The low frequency of heaps in areas of otherwise soil-free stone beds suggests that the

animals are largely unable to penetrate the stone beds themselves.

Intermound tunneling is presumably carried out in search of food plants. Pocket gophers of the genus *Thomomys* consume a broad range of root and shoot tissues. Ingles (1952) noted that in the California Sierras the rootstocks of *Lewisia nevadensis* were harvested and stored in caches by *T. monticola.* In eastern Washington, Daubenmire (1970) reported that rodents (probably *T. talpoides*) dug extensively in scabland soils, presumably for subterranean plant materials such as *Lomatium* roots. In northern Oregon, Moore and Reid (1951) found that removal of *T. talpoides* from mountain meadows over an eight-year period resulted in a several-fold increase in *Lomatium leptocarpum,* together with *Taraxacum officinale,* the roots of which were considered to be the favorite food of the pocket gopher. Thus, when available, the corms and roots of perennial plants are important foods of *T. talpoides.*

At the Lawrence Memorial Grassland Preserve the frequency of geophytes and fleshy-rooted hemicryptophytes is greater in the intermound zone than on the mounds, but the sparse vegetation of the stone beds is heavily dominated by such plants. Winward and Youtie (1978), for example, found only three species of geophytic perennial forbs, with a combined frequency of occurrence of 17 percent, in the sample plots from the *Festuca-Agropyron* community that dominates the mounds. On the mounds, pocket gophers eat the whole root systems of *Agropyron* and *Achillea* (D. B. Lawrence, pers. comm., 1986), and have probably eliminated most fleshy-rooted perennials. In the *Artemisia-Poa-Lomatium* community of intermound scabland, however, five species of fleshy-rooted perennials with a combined frequency of 72 percent were recorded by Winward and Youtie (1978). They noted that four geophytes dominated the stone beds: *Lomatium cous, L. minus, Delphinium nuttalianum,* and *Allium macrum.* The predominance of these species in intermound areas, and especially the stone beds, may result from lower accessibility to pocket gophers.

We suggest that the tunneling of pocket gophers in search of fleshy-rooted plants in the stony intermound soils is the primary mechanism that forms and maintains the sorted stone networks. The tunnel space created by tunneling beneath the stone nets and through the shallow intermound soil during dry periods is obliterated by settling of material from above during wet seasons. The downward movement of material is size-selective, the soil and smaller stones filtering downward most easily. The relatively greater downward movement of smaller stones creates the size-sorting that characterizes the beds. The soil fines and smallest stones (to the maximum size commonly mined and moved by pocket gophers) are ultimately removed and deposited on the mound surfaces, at the edges of stone beds, or on soil-and-rock islands, thus maintaining the fine textural composition of these areas. The lightly weathered, lichen-free stones that are present at the borders of many stone beds result from this deposition. Once a mature bed of stones larger than those that pocket gophers can mine has been formed it remains stable, and animal activity simply removes fine soil materials that are carried into the bed by erosion.

On level or nearly level sites, this mechanism leads to the formation of an encircling bed just beyond the mound edge, since animal activity is mound-centered, and soil conditions are similar in all directions. Where broad intermound areas form, because of thin soils that limit proximity of mounds to each other, polygonal nets may develop in which islands of soil and rock represent locations of less intensive tunneling and occasional deposition of soil mined from beneath the sorted stone beds.

How the mechanics of this process change with increase in slope is less clear. We suspect that it involves an intensification of the process responsible for the downslope pattern shown in Figure 2A. For a mound on a slope of few degrees, soil waterlogging during winter and spring will vary in severity around the margin. A mound impedes the movement of water moving downslope through the soil system, forcing the flow to become more concentrated along the sides of the mound (Figure 2B). Thus, the upper edge and sides of the mound will exhibit the wettest conditions, and the lower side will show a "moisture shadow." Excavation by pocket gophers appears to be greatest when and where soils are moist (Cox and Allen 1987), and thus the removal of soil may be greatest on the wetter lateral edges of mounds on slopes. The downslope extension of the lateral beds may reflect the downslope continuation of a wet soil zone that

favors soil mining and moundward translocation. This process may lead to the linkage of lateral stone beds of neighboring mounds up- and downslope, as well as to the linkage of the mounds themselves, creating the pattern of mounds and stone stripes commonly seen on slopes.

We therefore postulate that the origin of sorted stone circles and nets is intimately associated with that of Mima mounds on the Columbia Plateau, and that their formation and maintenance result from an interaction of soils, pocket gophers, and fleshy-rooted perennial plants.

Acknowledgments

We thank Catherine MacDonald, Oregon Land Steward, Nature Conservancy, for permission to carry out studies at the Lawrence Memorial Grassland Preserve, and for providing background information about the site. Annan Priday gave permission to collect soil samples from areas on the Priday Brothers ranch adjacent to the Preserve. Donald B. Lawrence provided advice and suggestions on the study and reviewed the manuscript in detail. We also thank R. F. Daubenmire, P. C. Lemon, T. L. Péwé, A. L. Washburn, and B. Youtie for criticism and suggestions on the manuscript. This study was supported by NSF grant INT-8420336 and by grant 211187 from the San Diego State University Foundation.

Literature Cited

Brunnschweiler, D. 1962. The periglacial realm in North America during the Wisconsin glaciation. Biul. Peryglacjalny 11:15-27.

Copeland, W. N. 1980. The Lawrence Memorial Grassland Preserve: A Biophysical Inventory with Management Recommendations. Unpublished report (revised 1983), Oregon Chapter, Nature Conservancy, Portland.

Cox, G. W. 1984. The distribution and origin of Mima mound grasslands in San Diego County, California. Ecology 65:1397-1405.

Cox, G. W., and D. W. Allen. 1987. Translocation of soil by pocket gophers in a Mima moundfield. Oecologia, 72:207-210.

Cox, G. W., and C. G. Gakahu. 1986. A latitudinal test of the fossorial rodent hypothesis of Mima mound origin in western North America. Zeitschrift für Geomorphologie 30:485-501.

Dalquest, W. W., and V. B. Scheffer. 1942. The origin of the Mima mounds of western Washington. J. Geol. 50:68-84.

Daubenmire, R. 1970. Steppe vegetation of Washington. Wash. Agric. Exp. Sta. Tech. Bull. 62.

Fosberg, M. A. 1965. Characteristics and genesis of patterned ground in Wisconsin time in a chestnut soil in southern Idaho. Soil Sci. 99:30-37.

Goldthwait, R. 1976. Frost sorted patterned ground: a review. Quaternary Res. 6:27-35.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle.

Ingles, L. G. 1952. The ecology of the mountain pocket gopher, *Thomomys monticola.* Ecology 33:87-95.

Johnson, C. B. 1982. Soil mounds and patterned ground of the Lawrence Memorial Grassland Preserve. Oregon State University, Corvallis, M. S. Research Paper.

Received 5 December 1986
Accepted for Publication 29 March 1987.

Kaatz, M. R. 1959. Patterned ground in central Washington: a preliminary report. Northw. Sci. 33:145-156.

Knechtel, M. M. 1952. Pimpled plains of eastern Oklahoma. Geol. Soc. Amer. Bull. 63:689-700.

Malde, H. E. 1961. Patterned ground of possible solifluction origin at low altitude in the western Snake River Plain, Idaho. U.S. Geol. Survey Prof. Pap. 424-B.

_____. 1964. Patterned ground on the western Snake River Plain, Idaho and its possible cold-climate origin. Geol. Soc. Amer. Bull. 75:191-207.

Masson, P. H. 1949. Circular soil structures in northeast California. Calif. Div. Mines Bull. 151:61-71.

Moore, A. W., and E. H. Reid. 1951. The Dalles pocket gopher and its influence on forage production of Oregon mountain meadows. USDA Circular No. 884.

Nelson, C. A. 1977. The origin and characteristics of soil mounds and patterned ground in north central Oregon. Oregon State University, Corvallis. M.S. Research Paper.

Pyrch, J. B. 1973. The characteristics and genesis of stone stripes in north central Oregon. Portland State University, Portland. M.S. Thesis.

Rossman, A. Y. 1977. Cryptogamic plants of the Lawrence Memorial Grassland Preserve. Unpublished report, Oregon Chapter, Nature Conservancy, Portland.

Scheffer, V. B. 1947. The mystery of the Mima mounds. Sci. Monthly 65:283-294.

Tallyn, L. A. K. 1980. Scabland mounds of the Cheney Quadrangle, Spokane County, Washington. Eastern Washington University, Cheney. M.S. Thesis.

Washburn, A. L. 1980. Geocryology—A Survey of Periglacial Processes and Environments. Edward Arnold, London.

Waters, A. C., and C. W. Flagler. 1929. Origin of small mounds on the Columbia River Plateau. Amer. J. Sci. 18:209-224.

Winward, A. H., and B. Youtie. 1978. Ecological inventory of the Lawrence Memorial Grassland Preserve. Proc. Ore. Acad. Sci. 14:50-65.

Zar, J. H. 1974. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs.

Charles M. Peven
P.U.D. No. 1 of Chelan County
P.O. Box 1231, Wenatchee, Washington 98801

Downstream Migration Timing of Two Stocks of Sockeye Salmon on the Mid-Columbia River

Abstract

Juvenile salmonids on the main-stem Columbia River must pass as many as nine dams on their seaward migration. Survival of smolts is a major concern to the various agencies that manage the salmonid resource in this area. Stocks of naturally reproducing sockeye salmon (*Oncorhynchus nerka*) migrating past Rock Island Dam originate from the Wenatchee and the Okanogan river systems. The nursery lakes for these sockeye juveniles are Lake Wenatchee and Lake Osoyoos, respectively. Data collected from Rocky Reach Dam (exclusively Osoyoos fish) confirms that fish greater than 100 mm fork length can generally be categorized as Osoyoos stock. Sockeye from the Lake Wenatchee system are predominantly smaller than 100 mm fork length. Smaller fish comprised the majority of migrants in April, whereas throughout May larger fish were more prevalent. The juvenile migration of sockeye past Rock Island Dam in 1986 was bimodal, with the first peak appearing in mid-April (primarily Wenatchee stock) and the second peak at the end of May (primarily Osoyoos stock). The difference in migration timing of these stocks at Rock Island Dam may be attributed to a greater migration distance for the Lake Osoyoos fish or possible later smoltification, or delay in down-stream movement the Osoyoos stock.

Introduction

Historically, there were eight sockeye salmon (*Oncorhynchus nerka*) nursery lakes in the Columbia River basin. Construction of Grand Coulee Dam blocked access to the upper river and sockeye spawning was limited to the Wenatchee and Okanogan river systems. A program designed to prevent the extinction of upper Columbia River salmonids was developed during the construction of Grand Coulee Dam. Returning adult salmon were trapped from the fishways at Rock Island Dam and transported to be spawned at either newly constructed federal hatcheries or in mid-Columbia tributary streams. Sockeye were transferred into the Wenatchee and Okanogan systems, where they were forced to spawn in streams above Lakes Wenatchee and Osoyoos. Others were spawned and reared at hatcheries, with juveniles released at the hatcheries or transplanted into Lakes Wenatchee and Osoyoos. The stocks of sockeye that presently inhabit these lakes are a mixture of both natural and introduced fish obtained during the Grand Coulee salvage operation more than 40 years ago (J. W. Mullan pers. comm.).

The objective of this study was to determine the relative timing of Lake Wenatchee and Lake Osoyoos stocks migrating past Rock Island Dam. Differences in the length frequency distributions of the two stocks provide a method for determining the relative frequency of each in a sample. Timing of the downstream migration of each stock was determined by plotting the daily catch rate at the Rock Island Dam juvenile bypass facility in 1986. Since sockeye smolts collected at Rocky Reach Dam can only be of Lake Osoyoos origin (the Wenatchee River confluence is downstream from Rocky Reach Dam), data collected at Rocky Reach Dam could be used to differentiate the length frequency distributions associated with the two stocks passing Rock Island Dam.

Methods

Downstream migrating salmonids were collected for identification and enumeration from the gatewell bypass trap at Rock Island Dam, riverkilometer 731.5 (rivermile 453.5), on the mid-Columbia River (Figure 1). Out-migrants, entering the gatewells from the turbine intakes passed through orifices into a bypass channel, and eventually into the trap tank. Fish in the trap passed over dewatering screens into a flume, where they were held overnight. The fish in the flume were moved via an elevator hopper to a 1.3 x 1.3 x .9 m portable fiberglass holding tank daily. The holding tank was supplied with a continuous flow of river water with a 5 hp submersible pump.

All fish collected in the trap were anesthetized with Tricaine Methane Sulfonate (MS 222). Fork length measurements taken from either the entire catch, or from a subsample of at least 100

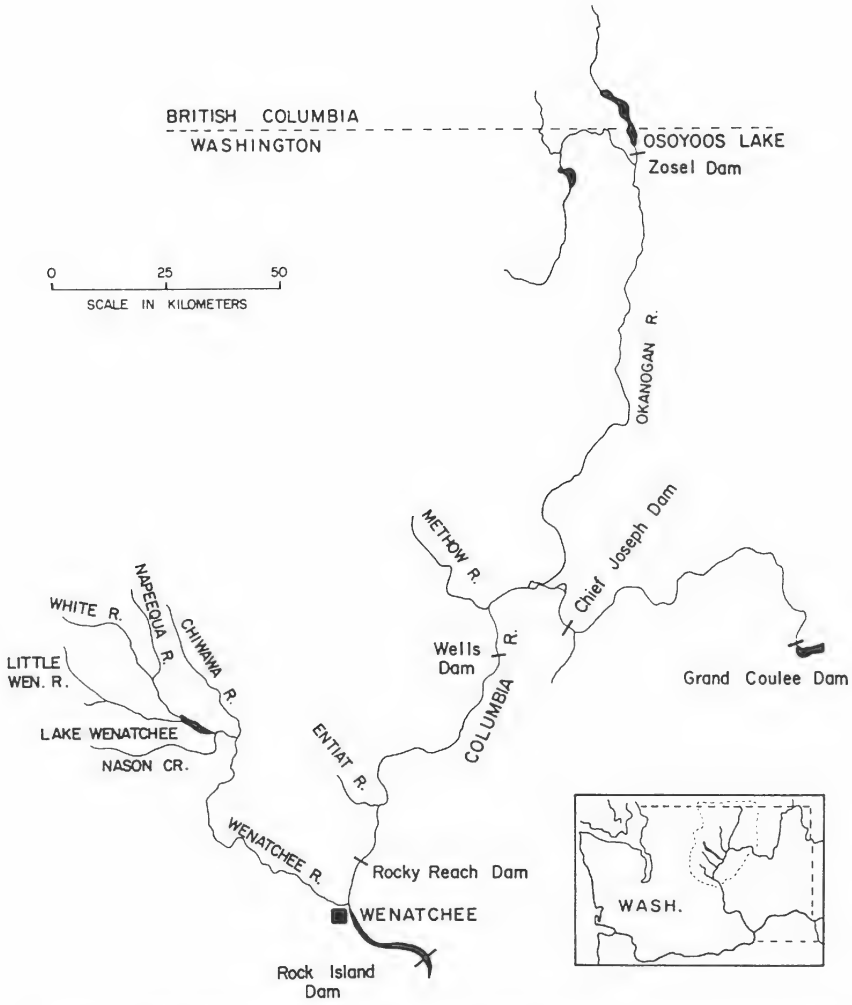

Figure 1. Columbia River and major tributaries between Grand Coulee Dam and Rock Island Dam.

when the daily catch was large. Measurements were recorded in 5 mm length classes. Examination of length frequencies indicated that 10 mm class boundaries were adequate for separation of the stocks. Sockeye lengths were sampled at Rocky Reach Dam in a similar manner where fish were collected from both fyke nets and a gatewell dipper basket.

Results

A total of 30,893 sockeye smolts was collected at the Rock Island Dam bypass trap between 8 April and 15 June, 1986. Daily collections ranged from 8-3,218 ($\bar{x}$ = 448). Nineteen percent (n = 5866) of the sockeye were sampled for length frequencies. Sample sizes ranged from 8-147 ($\bar{x}$ = 85) for the 69-day period.

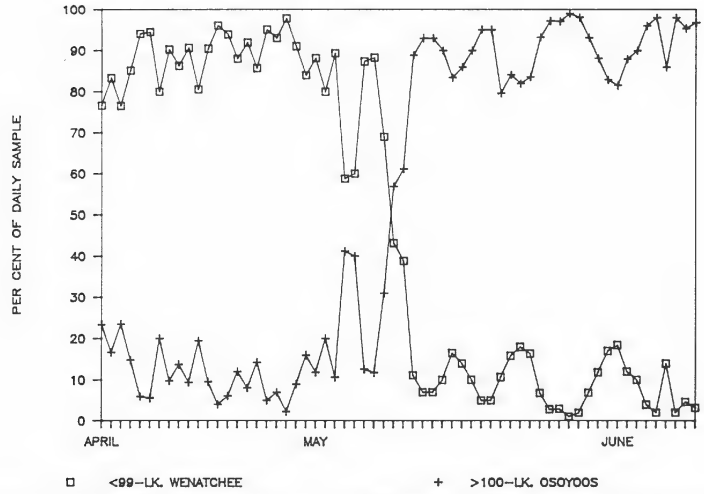

Figure 2. Estimated proportions of juvenile sockeye from Lakes Wenatchee and Osoyoos passing Rock Island Dam, 1986 (data after 8 June not included because of small sample sizes).

Sockeye length frequencies were taken from Osoyoos stock at Rocky Reach Dam (upstream from the Wenatchee River) on May 12, 13, 30, and June 2 (Figure 1). The length frequency of these samples and length data from previous studies (D. E. Weitkamp, J. A. McGee pers. comm.) show that most Osoyoos stock fish are $>$ 100 mm fork length.

At Rocky Reach Dam, 85 percent of the Osoyoos stock sockeye were $\geq$ 100 mm fork length. By contrast, 88.9 percent of the sockeye sampled at Rock Island Dam in April were $<$ 100 mm fork length. No samples limited to Lake Wenatchee sockeye were obtained for length frequency determination. However, the April catches of sockeye at Rock Island Dam appear to be of Lake Wenatchee stock, based on fork length and because sockeye comprised only 1.3 percent of 1,465 fish taken from the Rocky Reach prototype fish screen during April sampling in an earlier study (S. G. Hays pers. comm.).

A fork length of 100 mm separated the Wenatchee ($\leq$ 99 mm) from the Osoyoos ($\geq$ 100 mm) stocks, and provided the least degree of overlap in the length distributions. Potential misclassification of Osoyoos and Wenatchee stock using this criterion is 15 and 11 percent, respectively. Few ($<$ 0.3%) residual sockeye (fork length $>$ 130 mm) of the Wenatchee stock would be misclassified as Osoyoos stock.

Based on the length distribution of the daily catches, the majority of Lake Wenatchee fish had migrated past Rock Island Dam by the end of the first week in May, while Osoyoos fish began to make up more than 50 percent of the fish sampled per day by the first week in May (Figure 2). During May, 26 percent of the sockeye were $<$ 100 mm fork length, with most of the smaller fish caught during the first week of the month. Osoyoos fish predominated catches through the remainder of May and into June (Figure 2). This finding agrees with previous studies of Osoyoos stock run timing at Wells Dam (D. E. Weitkamp, J. A. McGee, and K. B. Truscott pers. comm.).

Discussion

Based on the data collected in 1986, sockeye smolts that migrate downstream from Lake Osoyoos are larger than out-migrants from Lake Wenatchee. Lake Osoyoos has a higher production of planktonic biomass than Lake Wenatchee (J. W. Mullan pers. comm.). This results in a higher smolt production (12.4 pounds/acre) in Lake Osoyoos than Lake Wenatchee (6.3 pounds/acre) (J. W. Mullan pers. comm.). The greater availability of food may also account for the larger size of the migrating Osoyoos stock.

The downstream migration of sockeye juveniles past Rock Island Dam during both 1985

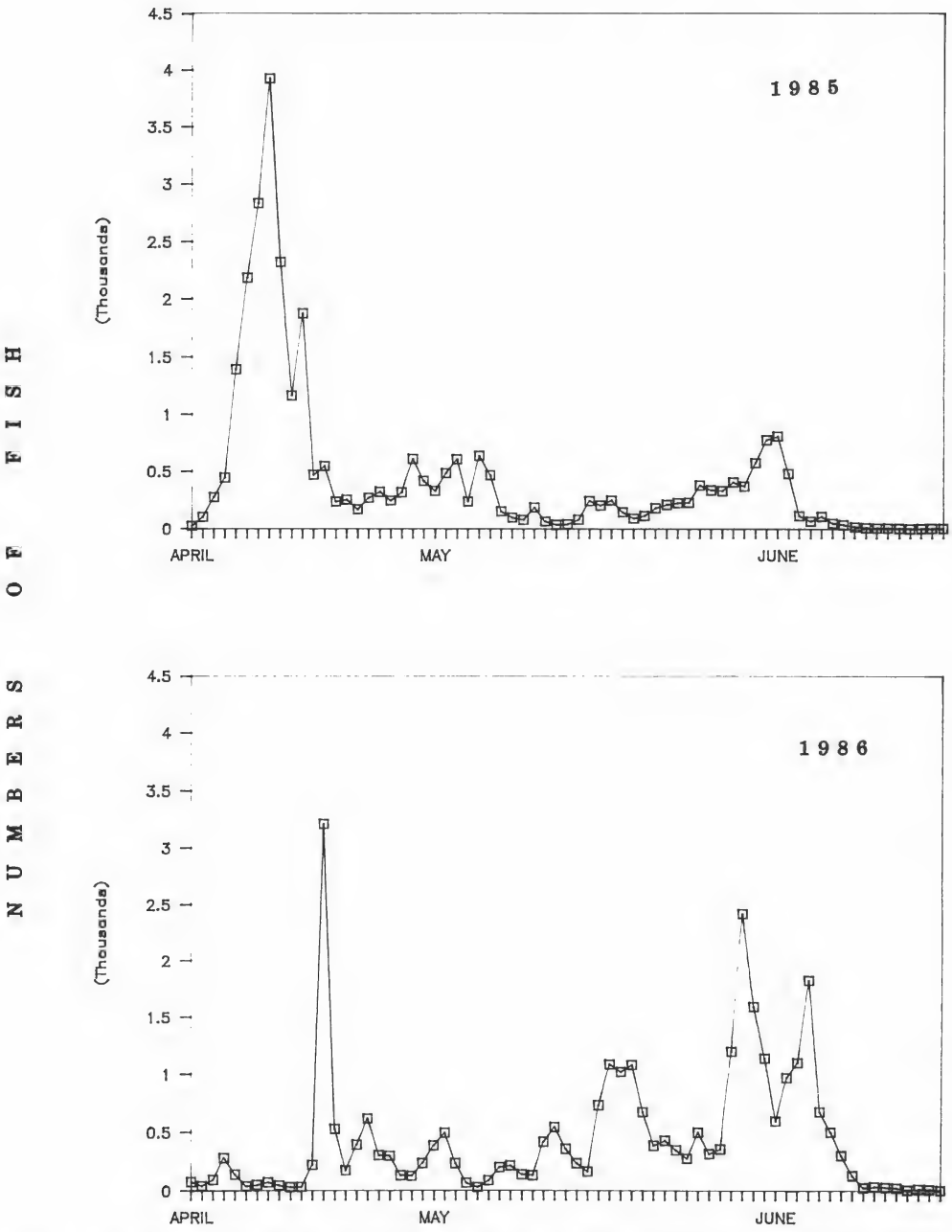

Figure 3. Daily catch numbers of sockeye salmon juveniles from the Rock Island Dam bypass trap for 1985 and 1986.

and 1986 was bimodal (Figure 3) with the peaks representing the two stocks of sockeye passing the dam. The length-frequency data indicate that the 1986 contribution of Osoyoos fish to the total run was larger than the 1985 contribution. Most of the out-migrants observed at Rock Island Dam in 1986 were from the 1984 brood year (S. G. Hays pers. comm.). In 1983, 30 percent of the returning sockeye adults were Osoyoos-bound fish, while in 1984, 67.2 percent of the returning adults were migrating to Lake Osoyoos. This supports the conclusion that the downstream migration of Osoyoos-reared sockeye smolts made up a larger portion of the 1986 run observed at Rock Island Dam than that in 1985 (Figure 3).

The difference in migration timing between the two stocks of sockeye may be attributed to a greater migration distance for the Lake Osoyoos stock, although previous studies (D. E. Weitkamp, J. A. McGee pers. comm.) have shown that Osoyoos fish do not start their annual migration until late April.

Later smoltification may also contribute to the difference in timing of the Osoyoos stock. Smoltification is initiated by a variety of factors, some of which include changes in temperature, photoperiod, stream flow, and lunar cycles (E. L. Brannon pers. comm.). Of these factors, stream flow and temperature regimes would influence the two stocks differently.

Only the relative proportion of each stock migrating past Rock Island Dam can be estimated from the numbers of fish caught at the bypass trap because there is no estimate of trap efficiency. Variables such as spill and power generation influence the numbers of juveniles caught in the bypass trap. Behavioral differences in the two stocks may also affect the efficiency of the daily catch.

Received 4 August 1986
Accepted for publication 30 March 1987

Acknowledgments

I would like to thank Dick Nason of Chelan County Public Utility District for initiating this study. Special thanks to Steve Hays for information and his thorough editing of the report. I am grateful to Paul Fielder for his help and reediting of this manuscript. Karol Danner and Meloney Hause were instrumental in collection of field data.

Christopher J. Norment
Department of Zoology and Charles R. Conner Museum
Washington State University, Pullman, WA 99164

A Comparison of Three Methods for Measuring Arthropod Abundance in Tundra Habitats and its Implications in Avian Ecology

Abstract

Arthropod abundance was sampled in the alpine tundra of the Beartooth Mountains, Wyoming during the summer of 1981. Sticky board and pitfall traps showed similar patterns of capture success, with maximum captures in late July; capture success using a sweep net showed a similar peak but fluctuated more than the other methods. Proportions of major taxa and size distribution of arthropods captured differed significantly between all three methods. Pitfall traps caught relatively more Coleoptera and Araneae. Sticky boards and sweep nets captured proportionately more Diptera. Sticky boards and pitfall traps caught a larger proportion of arthropods > 4 mm in length than did sweep nets, and significantly more taxa per sampling period than did sweep netting. Sweep netting was a poor technique for sampling surface-active tundra arthropods. A combination of pitfall traps and sticky boards sampled a wider variety of prey taxa and may provide a more accurate estimate of abundance. Researchers working in tundra habitats should use care in making ecological inferences related to prey availability based on capture data from a single sampling method, as multiple methods are required to adequately sample the tundra arthropod fauna.

Introduction

Temporal and spatial patterns of arthropod abundance may have important consequences for avian predators in arctic and alpine habitats. Arthropod abundance may influence avian breeding phenology, habitat use, and resource partitioning (Pitelka 1959, Holmes and Pitelka 1968, Hoffman 1974, Seastedt and MacLean 1979). Accordingly, several avian ecologists have attempted to measure patterns of arthropod abundance in tundra and meadow habitats. These attempts have generally involved a single relative method (MacLean and Pitelka 1971, Hussell 1972, Conry 1978, Seastedt and MacLean 1979, Winternitz 1980). Although relative techniques, which measure populations in unknown units, may accurately describe arthropod abundance, they are also subject to numerous interpretational and sampling problems (Southwood 1978).

The purpose of this paper is to compare the relative efficiency of using sticky boards, pitfall traps, and sweep nets to sample arthropod abundance in a high montane meadow. Temporal and spatial changes in abundance within and among taxa at the class or species level are not discussed. Rather, data on seasonal activity patterns, and size and order of arthropods captured, are used to evaluate the effectiveness of the three techniques, and to discuss implications for ornithological research. To my knowledge, a comparative study of this nature has not been previously undertaken in an alpine or arctic habitat.

Methods

Arthropods were sampled in a high montane meadow at 3000 m near the upper tree limit in the Beartooth Mountains, Park County, Wyoming (44°56'N, 109°30'W) during the summer of 1981. The study area contained three habitat types: 1) dry meadow, with short, sparse vegetation; 2) moist meadow, with vegetation intermediate in size and density; and 3) wet meadow, with tall, dense vegetation. This terminology follows that of Pattie and Verbeek (1966), although the plant communities did not correspond exactly to those described on the Beartooth Plateau; a major difference was that their "wet meadow" contained more willow (*Salix* spp.), which was almost absent from my study site.

Arthropods were sampled between 22 June and 14 August 1981. Twenty sticky boards (MacLean and Pitelka 1971) of 10 cm x 20 cm plexiglass coated with Tanglefoot™ were placed at ground level using a grid established for bird censusing and coordinates chosen with a random numbers table. Single pitfall traps (7.5 cm diameter plastic cups) were buried flush with the ground surface at 1 m from the center of each sticky board. Ethylene glycol was used as a preservative. Sweep netting was conducted along a 200 m transect through the area sampled with

[1]Present address: Westover School, Middlebury, CT 06762

sticky boards and pitfall traps; 200 sweeps were taken along each transect.

Sticky boards and pitfall traps were operated simultaneously for 24 hr at about one-week intervals. Sweep net transects were run at 1200 MST on days that arthropods were collected from traps. All arthropods captured were identified to order, measured and assigned to size class categories (2.1-4.0, 4.1-6.0, . . . 18.1-20.0, > 20.0 mm). Arthropods < 2.1 mm in length were not counted, as tundra-foraging birds rarely capture smaller prey (Holmes and Pitelka 1968, Hussell 1972, Seastedt and MacLean 1979). Analyses of taxonomic and size class composition are based upon total captures during the study. The G-statistic (Sokal and Rohlf 1981) was used to compare differences in capture frequencies for taxa and size class categories among the methods.

Results

Sticky board and pitfall traps showed similar capture success, with maximum captures between 13 July-31 July for pitfall traps and 24 July-31 July for sticky boards (Figure 1). The abundance peak was broader for pitfall traps, with a greater proportion of captures earlier in the season. Sweep net captures peaked on 24 July, dropped sharply on 31 July and 7 August, then rose; this fluctuation was not mirrored by sticky boards and pitfall traps.

Pitfall traps captured significantly different proportions of arthropod taxa than either sticky boards or sweep netting (Tables 1, 2; G-tests, $P < .001$). Proportions of major taxa captured also differed significantly between sticky boards and sweep nets (G-test, $P < .001$), but differences were not as great (Table 2). The most common taxa captured in pitfall traps were Araneae (entirely Arachnida), Diptera and Coleoptera (Table 1). Diptera, Hymenoptera, and Homoptera (mostly Cicadellidae) were the most common orders captured by sticky boards and sweep netting. Between-method comparisons using Kendall's rank correlation (Sokal and Rohlf 1981) indicated concordance of taxa ranked according to total

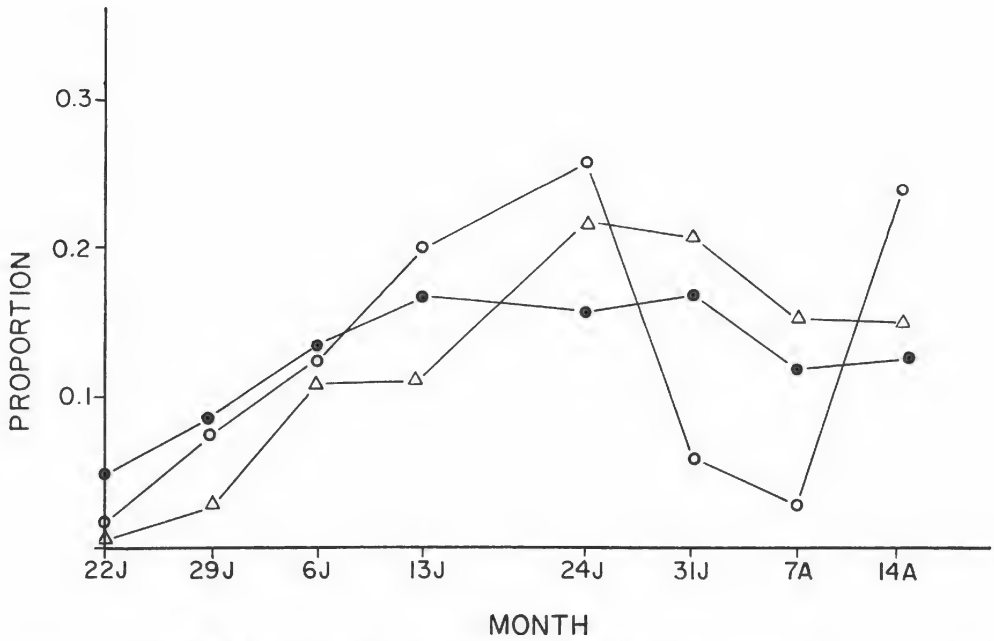

Figure 1. A comparison of abundance patterns of surface-active arthropods as measured by sweep net (○), sticky board (△), and pitfall trap (●) between 22 June and 14 August 1981. Proportions are based on total number of arthropods captured by each method.

TABLE 1. Proportion of total arthropods in each order captured by sweep net (SN), sticky boards (SB) and pitfall traps (PF); n = total captures over sampling period.

Sampling		Order								
Method	n	Araneae	Orthoptera	Hemiptera	Homoptera	Lepidoptera	Diptera	Coleoptera	Hymenoptera	Other*
SN	887	.007	.003	.028	.063	.002	.847	.001	.037	.010
SB	6651	.007	.019	.005	.049	.047	.806	.002	.064	.000
PF	1651	.307	.040	.040	.031	.010	.260	.219	.053	.039

*Includes Acarina, Tricoptera, and unidentified arthropods.

number of captures for sticky boards and sweep netting ($\tau = 0.611$, $P < .05$). Rankings of orders captured in pitfall traps were not concordant with those captured by sticky boards ($\tau = 0.084$, $P > .05$) and sweep netting ($\tau = 0.084$, $P > .05$).

TABLE 2. G-values for between-method comparisons of taxonomic and size-class composition of captures for sweep net (SN), sticky boards (SB) and pitfall traps (PF). All taxonomic and size-class values are significantly different at the .001 level.

	Comparison		
	SB-PF	SB-SN	SN-PF
Taxonomic Composition	3253.640	131.880	1143.468
Size-class Composition	169.540	137.860	201.498

Abundance patterns of Araneae and Coleoptera, as measured by pitfall traps, showed broad peaks, with only moderate weekly changes in capture success (Figure 2). Fluctuations in numbers of these orders captured on sticky boards were much greater, perhaps because of small sample sizes. Abundance patterns for other common arthropod orders were similar for sticky boards and pitfall traps (Figures 2, 3). Numbers of Araneae, Coleoptera, Lepidoptera, and Orthoptera captured in sweep nets were inadequate to show changes in abundance during the sampling period. Numbers of Diptera, Homoptera, and Hymenoptera showed different peaks and fluctuated more severely than did numbers of these orders captured by pitfall traps and sticky boards. Sweep netting also captured significantly fewer orders during each trapping period than did either pitfall traps or sticky boards [Tukey-Kramer Method (Sokal and Rohlf 1981); $P < .05$ for both comparisons].

Size frequency distributions of captured arthropods (Table 3) differed significantly among all inter-method comparisons (Table 2). Pitfall traps captured higher proportions of arthropods in size categories > 6.1 mm than did sweep netting or sticky boards, while sweep netting captured a higher proportion of arthropods in the 2.1-4.0 mm range than did the other methods.

Discussion

The trapping efforts in this study yielded results similar to those from studies elsewhere. Beetles and spiders are important ground surface predators in Colorado and Norwegian alpine tundra, and are caught frequently in pitfall traps (Tolbert *et al.* 1977, Hågvar *et al.* 1978). In both areas, these taxa display early and late season

TABLE 3. Proportion of total arthropods in each size class captured by sweep net (SN), sticky boards (SB) and pitfall traps (PF); n = total captures over sampling period.

Sampling		Size Class (mm)					
Method	n	2.1-4.0	4.1-6.0	6.1-8.0	8.1-10.0	10.1-12.0	> 12.1
SN	887	.543	.323	.103	.019	.011	.001
SB	6651	.355	.452	.108	.036	.025	.023
PF	1651	.302	.361	.217	.065	.025	.030

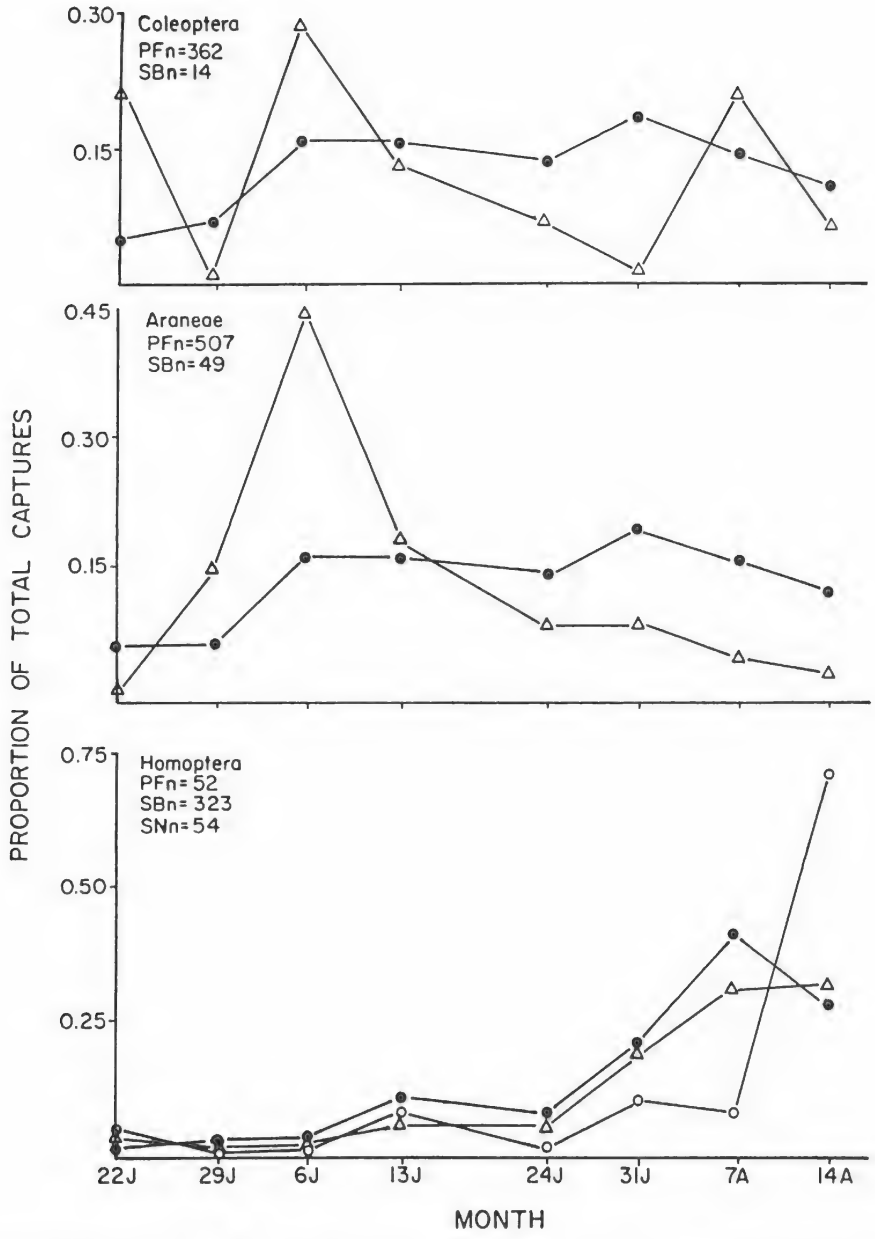

Figure 2. Abundance patterns of Coleoptera, Araneae, and Homoptera captured by sweep net (SN, ○), sticky board (SB, △), and pitfall trap (PF, ●) between 22 June and 14 August 1981. Sample sizes for the methods are given for each order. Proportions are based on the total number of arthropods captured by each method.

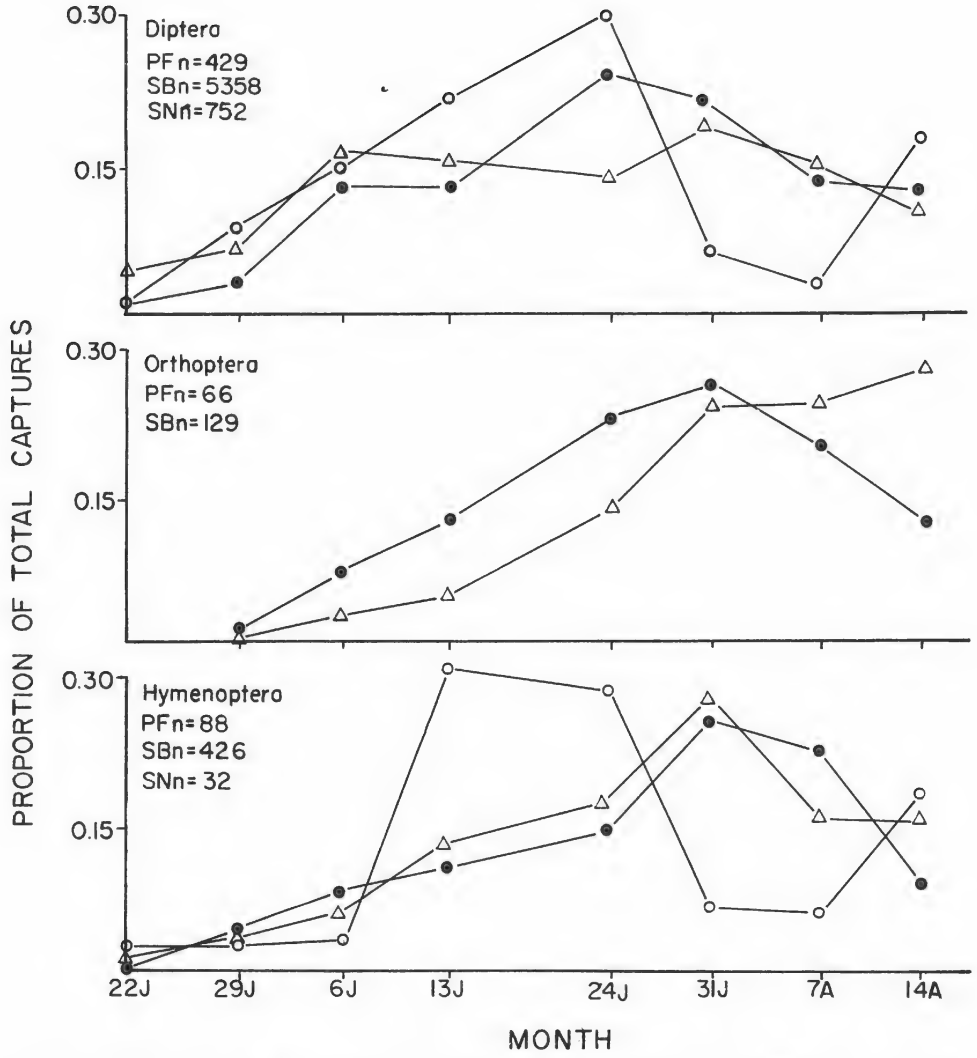

Figure 3. Abundance patterns of Diptera, Orthoptera, and Hymenoptera captured by sweep net (SN, ○), sticky board (SB, △), and pitfall trap (PF, ●) between 22 June and 14 August 1981. Sample sizes for the methods are given for each order. Proportions are based on the total number of arthropods captured by each method.

abundance peaks. As in the present study, Hågvar *et al.* (1978) and Norvell (1985) captured large numbers of Diptera and Hymenoptera in pitfall traps. In a study using sticky boards in Colorado alpine tundra, dipterans were captured 15 times more frequently than any other order (Conry 1978).

Arthropod populations are difficult to measure accurately (Southwood 1978). While data from absolute methods (suction sampling, direct

count, Berlese-funnel), which measure populations in numbers of animals/unit area (Southwood 1978), are preferable to those from relative methods, ornithologists may lack the time or equipment necessary to accurately quantify arthropod populations. Thus there is a need for relative methods that require simple equipment and less time (Southwood 1978), yet accurately depict activity patterns of arthropod prey.

The results of this study and those collected elsewhere can be used to make recommendations regarding the use of sweep nets, pitfall traps, and sticky boards in tundra habitats. Of these methods, sweep netting seems to be the least effective. Total number of captures was lowest, and some orders of ground-dwelling arthropods were missed almost entirely. This method was also more vulnerable to disruption by short-term changes in weather conditions (high winds or afternoon convectional storms) than either pitfall traps or sticky boards, which were operated for 24-hr periods. In addition, experience of the collector may also influence the results obtained by sweep nets (W. J. Turner, Washington State University, pers. comm.). These limitations make sweep netting an unreliable technique for estimating arthropod activity, although it has been used for this purpose in a Colorado montane meadow (Winternitz 1980).

Pitfall traps are useful in illustrating seasonal variations in activity of different taxa of surface-active arthropods (Uetz and Unzicker 1976, Hågvar *et al.* 1978), although the data are subject to interpretational errors (Uetz and Unzicker 1976, Adis 1979). Thus, it is not surprising that Araneae and Coleoptera were captured frequently in pitfall traps during the study. However, pitfall traps may yield little information on flying arthropods. In this study, few Lepidoptera and Homoptera were captured using this method, even though both taxa include important foliage herbivores in alpine tundra (Tolbert *et al.* 1977). Diptera were probably also underrepresented in these samples, as they comprised 27 percent of the total pitfall captures, versus 80 percent of all sticky board captures.

In this study, sticky boards were most effective in capturing flying and/or hopping arthropods, as has been found in other studies of tundra arthropods (MacLean and Pitelka 1971, Conry 1978). Hadley (1969) has shown that sticky traps and direct enumeration give similar information on emergence patterns for a tipulid in a British bog. Other important taxa of surface-active arthropods were probably underrepresented, particularly Coleoptera and Araneae. These taxa are important components of other alpine tundra faunas (Tolbert *et al.* 1977, Hågvar *et al.* 1978) and were taken frequently in pitfall traps. Conry (1978) trapped few spiders on sticky boards in Colorado alpine tundra, while MacLean and Pitelka (1971) trapped few ground beetles on sticky boards in arctic Alaskan tundra.

Estimates of arthropod activity and emergence patterns in tundra and meadow habitats, based on data from a single capture method, have been used to make inferences regarding avian ecology in a number of studies. Since any one method will not sample all types of available arthropod prey adequately, such inferences may be misleading. For example, Conry (1978) captured few arthropods early in the season on sticky boards. On this basis, she hypothesized that Water Pipit (*Anthus spinoletta*) populations were most likely limited by early-season food shortages. However, other studies show that sticky boards do not adequately sample spiders and ground beetles, which are relatively abundant in the alpine in early season (Tolbert *et al.* 1977, Hågvar *et al.* 1978, present study). Although Water Pipit diets have not been studied intensively throughout the breeding season in the North American alpine, spiders and ground beetles are important components of early season Meadow Pipit (*Anthus pratensis*) diets in the Norwegian alpine (Hågvar and Østbye 1976), and Conry (1978) found that Water Pipits frequently fed their nestlings spiders. Thus Conry's inference cannot be supported because her sampling method missed an important, and possibly abundant, component of pipit diets.

A second example in which an important component of the diet of a tundra-nesting species may have been sampled inadequately is found in Hussell's (1972) comparison of arthropod abundance and hatching dates for Snow Buntings (*Plectrophenax nivalis*). In both 1968 and 1969, a large number of bunting broods hatched prior to the emergence of flying arthropods captured by sticky boards. Presumably, nestlings from these broods would have been fed other kinds of arthropod prey, including larvae, pupae, and spiders, which are an important early-season food source for buntings on Devon Island (Pattie

1977), but the sampling method was ineffective in capturing these forms.

From the above discussion, several recommendations can be made. First, ornithologists seeking to estimate arthropod prey activity should use more than one relative method. Uetz and Unzicker (1976) and Adis (1979) suggested that studies using pitfall traps should employ a second method to reduce interpretational problems. Holmes (1966) used four sampling techniques in a study of the feeding ecology of the Dunlin (*Calidris alpina*) in arctic Alaska; each method was selected to sample an important dietary component. Such decisions can only be made on the basis of at least a partial understanding of the natural history of both the avian predator and its prey.

Selection of a single sampling technique requires sufficient information to justify such a decision. The conclusions of Custer and Pitelka (1977) and Seastedt and MacLean (1979) concerning the impact of temporal and spatial patterns of prey abundance on Lapland Longspur (*Calcarius lapponicus*) breeding ecology were based entirely on data from sticky board captures. However, dietary analyses showed that the major longspur prey taxa are sampled by sticky boards, validating their conclusions.

Second, sweep netting is not an appropriate technique for obtaining indices of relative arthropod abundance in tundra habitats. It seriously underestimates some important prey taxa, and is more influenced by inclement weather.

Third, a combination of sticky boards and pitfall traps will probably give an accurate estimate of the relative abundance of adult arthropods through time in tundra habitats. However, sampling of immature forms, which may constitute an important dietary component of some tundra-breeding species (Hågvar and Østbye 1976, Conry 1978, Seastedt and MacLean 1979), would require the use of an absolute sampling method.

Acknowledgments

I thank D. P. Hendricks, R. E. Johnson, W. J. Turner, and two anonymous reviewers for commenting on an earlier draft of this manuscript. M. J. Norment and G. G. Norment provided help with the field work. P. Bugle answered a question regarding the statistical analyses. The study was supported by the Frank M. Chapman Memorial Fund, Sigma Xi, and the Graduate School of Washington State University.

Literature Cited

Adis, J. 1979. Problems of interpreting arthropod sampling with pitfall traps. Zool. Anz. 202:177-184.

Conry, J. A. 1978. Resource utilization, breeding biology and nestling development in an alpine tundra passerine community. University of Colorado, Boulder. Ph.D. Dissertation.

Custer, T. W., and F. A. Pitelka. 1977. Demographic features of a Lapland Longspur population near Barrow, Alaska. Auk 94:505-525.

Hadley, M. 1969. The adult biology of the crane-fly *Molophilus ater* Meigen. J. Anim. Ecol. 38:765-790.

Hågvar, S., and E. Ostbye. 1976. Food habits of the meadow-pipit, *Anthus pratensis* (L.), in alpine habitats at Hardangervidda, south Norway. Nor. J. Zool. 24:53-64.

Hågvar S., E. Østbye, and J. Melåen. 1978. Pitfall catches of surface-active arthropods in some high-mountain habitats at Finse, south Norway. II. General results at group level, with emphasis on Opiliones, Areneida, and Coleoptera. Norw. J. Ent. 25:196-205.

Hoffman, R. S. 1974. Terrestrial vertebrates. *In* J. D. Ives and R. G. Barry (eds.) Arctic and Alpine Environments. Methuen and Co., London. Pp. 475-568.

Holmes, R. T. 1966. Feeding ecology of the red-backed sandpiper (*Calidris alpina*) in arctic Alaska. Ecology 47:32-45.

Holmes, R. T., and F. A. Pitelka. 1968. Food overlap among coexisting sandpipers on northern Alaska tundra. Syst. Zool. 17:305-318.

Hussell, D. J. T. 1972. Factors affecting clutch size in arctic passerines. Ecol. Monogr. 42:317-364.

MacLean, S. F., Jr., and F. A. Pitelka. 1971. Seasonal patterns of abundance of tundra arthropods near Barrow. Arctic 24:19-40.

Norvell, J. R. 1985. Foraging sites of alpine birds in relation to snow accumulation. Towson State University, Towson, Maryland. M.S. Thesis.

Pattie, D. L. 1977. Population levels and bioenergetics of arctic birds on Truelove Lowland. *In* L. C. Bliss (ed.) Truelove Lowland, Devon Island, Canada: a high arctic ecosystem. Univ. Alberta Press, Edmonton. Pp. 423-436.

Pattie, D. L., and N. A. M. Verbeek. 1966. Alpine birds of the Beartooth Mountains. Condor 68:167-176.

Pitelka, F. A. 1959. Numbers, breeding schedule, and territoriality in Pectoral Sandpipers in northern Alaska. Condor 61:161-184.

Seastedt, T. R., and S. F. MacLean. 1979. Territory size and composition in relation to resource abundance in Lapland Longspurs breeding in arctic Alaska. Auk 96:131-142.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Second ed. W. H. Freeman, San Francisco.
Southwood, T. R. E. 1978. Ecological methods. Halsted Press, New York.
Tolbert, W. W., V. R. Tolbert, and R. E. Ambrose. 1977. Distribution, abundance, and biomass of Colorado alpine tundra arthropods. Arctic and Alp. Res. 9:221-234.
Uetz, G. W., and J. D. Unzicker. 1976. Pitfall trapping in ecological studies of wandering spiders. J. Arachnol. 3:101-111.
Winternitz, B. L. 1980. Birds in aspen. Management of western forests and grasslands for nongame birds. USDA For. Ser. Gen. Tech. Rep. Int-85. Pp. 247-257. Rocky Mtn. For. Range Exp. Sta. and Intermountain Region, Ogden, Utah.

Received 20 November 1986
Accepted for publication 6 April 1987

D. Chris Ritchie, Ritchie Environmental Consulting
North Vancouver, B.C., Canada V7M 1S8

Alton S. Harestad, Department of Biological Sciences
Simon Fraser University, Burnaby, B.C., Canada V5A 1S6

and

Ralph Archibald, Wildlife Branch, Ministry of Environment and Parks
Victoria, B.C., Canada V8X 1X5

Glyphosate Treatment and Deer Mice in Clearcut and Forest

Abstract

Prior to planting conifers, herbicides are commonly used to reduce competition from deciduous trees and shrubs. Herbicides are usually not toxic to wildlife but do affect their habitats. We examined deer mice (*Peromyscus maniculatus*) to assess the impact of herbicides on small mammals. Deer mice from adjacent untreated and glyphosate-treated clearcuts had similar body sizes and numbers of placental scars and foeti. In untreated clearcut, deer mice were more abundant than in treated clearcut, but were less abundant than in surrounding old growth forest. Glyphosate altered vegetation and reduced density of deer mice in young seral stages. Habitat changes induced by glyphosate likely modified abundance and quality of food and cover for small mammals.

Introduction

Use of herbicides for intensive forest management is increasing rapidly in British Columbia (von Schuckmann 1986). Herbicides are used to reduce competition from deciduous trees and shrubs on overgrown sites prior to planting conifers and for "conifer release" in older plantations. Glyphosate (Roundup®) is a commonly used herbicide because it kills deciduous vegetation rapidly, but does not usually harm conifers (Sutton 1978). Glyphosate also has low toxicity to humans and wildlife.

While herbicide toxicity to wildlife is seldom a problem, herbicides alter vegetation. These habitat changes and their accompanying impact on small mammals vary with habitat type and species. Abundance of small mammals can be reduced by herbicide treatment (Johnson and Hansen 1969, Hooven and Black 1976), remain unaffected (Sullivan and Sullivan 1982) or increased (Anthony and Morrison 1985).

We examined the effect of glyphosate treatment in a clearcut on the body characteristics and population indices of deer mice (*Peromyscus maniculatus*). Other studies have reported the effects on small mammals of herbicides applied to clearcuts several years after logging (Borrecco *et al.* 1979, Sullivan and Sullivan 1982). Our study was conducted on a site treated with glyphosate two years after logging, a seral stage not reported elsewhere.

Study Area and Methods

The study area is 50 km west of Kelsey Bay on northern Vancouver Island, British Columbia. It is situated in the wet subzone of the Coastal Western Hemlock Biogeoclimatic Zone (Klinka *et al.* 1979) and includes a 54 ha clearcut and surrounding old growth forest at an elevation of 500 m with a southwest aspect.

Three habitat types were examined in the study area: old growth forest, untreated clearcut and herbicide treated clearcut. After logging in 1983, approximately 70 percent of the clearcut was treated with glyphosate in fall 1985. A 21 ha portion of the clearcut was aerially sprayed with glyphosate at 1.2 kg/ha of active ingredient and an adjacent 17 ha area was handsprayed at 1.1 kg/ha of active ingredient. Plant species composition was determined for 10 randomly selected circular plots (10 m in diameter) in each habitat type. Ocular estimates were obtained for percent cover of the canopy, understory and ground layers, and each major plant species.

Small mammals were snap-trapped between 15 and 27 July 1986. Traps were baited with a mixture of peanut butter and oatmeal and placed at 10 m intervals along straight line transects 10 m apart through each habitat type. Transect

lengths varied with size of the cutblock, but were generally 250 m long. Traps were set overnight, and trapping was conducted approximately every other night, usually in all three habitat types. Of the 1661 total trapnights, 550 were in the forest, 558 were in the untreated clearcut and 553 were in the treated clearcut. Transect lines were moved daily to avoid retrapping of areas. Each trapped mammal was weighed and standard measurements were taken. Reproductive tracts were removed from females and examined for placental scars and foeti. Deer mice were classified by body weight as juvenile ($\leq$16 g) or adult (>16 g) (Sullivan and Sullivan 1982).

Results

Vegetation differed among the three habitat types. The forest had a dense canopy (83%) composed of amabilis fir (*Abies amabilis*) and western hemlock (*Tsuga heterophylla*) and a moderate understory (38%), composed of tall blue huckleberry (*Vaccinium ovalifolium*) and small conifers (Table 1). The forest had moderate slopes (40%), steeper than those in the clearcut (15%).

The untreated clearcut had no canopy, and a relatively dense understory (52%) dominated by tall blue huckleberry (27%), red elderberry (*Sambucus racemosa*) (10%) and fireweed (*Epilobium angustifolium*) (10%). The ground was covered with logging debris (29%) and lesser amounts of ferns and forbs (24%).

TABLE 1. Percent cover of vegetation and other ground cover in forest, untreated clearcut and clearcut treated with glyphosate near Kelsey Bay, B.C.

	Forest	Untreated Clearcut	Treated Clearcut
Canopy layer (>9.0 m)	83	0	0
Understory layer (0.3-9.0 m)	38	52	22
Tall blue huckleberry *Vaccinium ovalifolium*	23	27	5
Salmonberry *Rubus spectabilis*	0	3	6
Red elderberry *Sambucus racemosa*	0	10	2
small conifers	12	2	3
Fireweed *Epilobium angustifolium*	0	10	6
Other	3	0	0
Ground layer (<0.3 m)	24	19	32
Forbs	16	14	25
Ferns	8	5	7
Debris and litter	14	29	46

The treated clearcut had a relatively sparse understory (22%) composed of tall blue huckleberry (5%), salmonberry (*Rubus spectabilis*) (6%) and fireweed (6%). The ground was covered with greater amounts of logging debris (46%) and forbs and ferns (32%) than the untreated clearcut.

From 15 to 27 July, 307 small mammals were trapped during a total of 1661 trapnights. The majority (285/307) of mammals caught were deer mice. Because of the small representation of other species, they are omitted from further analyses. There was a significant difference in catch per unit effort (measured as the number of mice captured/trapnight) among habitat types ($F = 153.63$, $P \leq 0.05$). Catch per unit effort was 0.29 (155 deer mice/550 trapnights) in the old growth forest, 0.18 (82 deer mice/558 trapnights) in the untreated clearcut, and 0.10 (48 deer mice/555 trapnights) in the treated clearcut. Catch per unit effort can be used as an estimate of relative density. Below a value of 0.20, the relationship between catch per unit effort and density is approximately linear. For values exceeding 0.20, the index must be transformed (Leslie and Davis 1939). The transformed relative densities for old growth forest:untreated clearcut:treated clearcut were 1.00:0.53:0.29 respectively.

Sex ratio and age structure of deer mice (Table 2) were not significantly different among habitat types ($F = 0.48$, $P > 0.05$). No significant difference was detected among habitat types for body length or mass. Tail length was significantly greater in the forest habitat ($F = 29.28$, $P \leq 0.05$) and may reflect microsite differences in allometric growth. The number of placental scars was not significantly different among habitat types ($F = 0.94$, $P > 0.05$). However the number of foeti was significantly smaller in the forest habitat ($F = 12.62$, $P \leq 0.05$).

Discussion

Glyphosate does not affect reproductive rates of deer mice (Wahlgren 1979, Sullivan and Sullivan 1982). Sullivan and Sullivan (1982) used proportion of population breeding and juvenile recruitment as indices of reproductive rate. Although they were more concerned about direct effects of glyphosate, they did not detect significant differences in reproductive rates or growth of deer mice. Our results corroborate these previous

TABLE 2. Measurements and population characteristics of deer mice (*Peromyscus maniculatus*) trapped in forest, clearcut, and clearcut treated with glyphosate near Kelsey Bay, B.C. Sample size in parentheses. For each adult measurement, means followed by different letters are significantly different ($P \leq 0.05$). M = males, F = females.

		Forest			Untreated Clearcut			Treated Clearcut		
n		155			73			48		
Sex Ratio (M/F)		0.96			1.09			1.18		
% Juveniles		0.37			0.23			0.31		
Adult Measurements		$\bar{X}$	±SD		$\bar{X}$	±SD		$\bar{X}$	±SD	
Mass	F	18.5 a	1.4	(43)	21.1 a	4.1	(25)	20.5 a	2.5	(13)
(g)	M	18.3 a	1.4	(52)	18.4 a	1.5	(30)	19.2 a	2.1	(19)
Total length	F	188.4 a	9.2	(43)	173.8 b	8.4	(25)	173.7 b	7.0	(13)
(mm)	M	188.3 a	10.8	(52)	172.7 b	10.9	(30)	170.4 b	6.6	(19)
Body length	F	90.5 a	5.5	(43)	88.8 a	6.3	(25)	89.6 a	5.3	(13)
(mm)	M	89.6 a	5.7	(52)	87.6 a	5.7	(30)	89.7 a	4.9	(19)
Placental scars		3.2 a	2.4	(43)	2.3 a	2.2	(24)	2.1 a	2.3	(13)
Foeti		0 a	0.0	(43)	1.4 b	2.1	(24)	1.9 b	2.2	(13)

studies. We conclude that glyphosate treatment does not affect reproductive rates or body size of deer mice inhabiting young clearcuts in the Coastal Western Hemlock Biogeoclimatic Zone.

We observed significantly fewer foeti in deer mice from the forest. The mean number of placental scars was greater in deer mice from the forest but not significantly different from clearcuts. The presence of fewer foeti suggests that deer mice in the forest were breeding earlier than mice in clearcuts. Van Horne (1981) reported that high population density of deer mice may result in both a shorter and an earlier breeding season. Our results differ from those of Sadlier (1974) who found no differences in reproductive rate of deer mice in old growth forest and clearcuts.

The three habitat types in our study differed in density of deer mice. Transformed relative density of deer mice in the forest exceeded, by 87 percent, that in the untreated clearcut which in turn exceeded, by 83 percent, that in the treated clearcut. In some areas low densities of deer mice in clearcuts, relative to old growth forest, persisted for several years following logging (Harris 1968). In other areas, there was no difference in density of deer mice inhabiting mature forest and recent clearcuts (Petticrew and Sadlier 1974). Habitat differences could account for disparities among studies reporting densities of deer mice inhabiting forests and clearcuts. Slash burning, age of seral stage, and amount of logging debris could influence abundance of deer mice.

The density of deer mice in a 20-year-old plantation was not significantly different after glyphosate treatment (Sullivan and Sullivan 1982). However, density of deer mice in our untreated clearcut was greater than that in the treated clearcut. Perhaps differences in seral stages are responsible for the different results. The study by Sullivan and Sullivan (1982) was conducted on an older seral stage, a 20-year-old plantation. Conifers remaining after herbicide treatment may have been sufficient to provide thermal and concealment cover for small mammals. In addition, conifer seeds may have substituted for loss of food plants killed by glyphosate. Because of the sparcity of vegetation on the treated clearcut in our study, reduced amounts of food and cover would be available to deer mice, especially during winter when annual plants are dead and other plants buried by snow. Food abundance

affects populations of deer mice (Gashwiler 1979) and may be a factor in differences in density of deer mice among habitats near Kelsey Bay.

Anthony and Morrison (1985) report little impact of glyphosate on small mammal populations in Oregon. Only creeping vole (*Microtus oregonii*) was affected by glyphosate treatment. Abundance of creeping vole increased after herbicide treatment but there were no differences in abundance of other species, including deer mice. Anthony and Morrison (1985) concluded that an increase in grass due to shrub defoliation favoured creeping voles. Our site lacked the grass component prominent in the Oregon study. Of the 307 small mammals trapped near Kelsey Bay, only three were Townsend voles (*Microtus townsendii*) and they were captured in the treated clearcut.

Besides habitat factors, differences in size of study area contribute to differences in results between this study and that of Sullivan and Sullivan (1982). The treated clearcuts monitored in our study were larger than those studied by Sullivan and Sullivan (1982), >17 ha vs 4.9 ha. These larger areas reduce the effects of immigration and thus more accurately reflect population changes due to glyphosate treatment at operational scales.

Glyphosate treatment of the clearcut reduced percent cover and species composition of the understory layer. These changes may have affected the seasonal availability of food and cover important to deer mice and contributed to decreased densities of deer mice. Herbicide treatments appear to have different impacts in different seral stages. In young seral stages densities of deer mice are reduced, whereas in older seral stages deer mice are not affected.

Acknowledgments

The British Columbia Trappers' Association and the Wildlife Branch of the British Columbia Ministry of Environment provided support. We thank Mr. G. Whalley for field assistance.

Literature Cited

Anthony, R. G., and M. L. Morrison. 1985. Influence of glyphosate herbicide on small mammal populations in western Oregon. Northw. Sci. 59:159-168.

Borrecco, J. E., H. C. Black, and E. F. Hooven. 1979. Response of small mammals to herbicide-induced habitat changes. Northw. Sci. 53:97-106.

Gashwiler, J. S. 1979. Deer mouse reproduction and its relationship to the tree seed crop. Amer. Midl. Nat. 102:95-104.

Harris, A. S. 1968. Small mammals and natural reforestation in southeast Alaska. USDA For. Serv. Res. Note PNW-75. Pac. Northw. For. Range. Exp. Stn., Portland, Oregon.

Hooven, E. F., and H. C. Black. 1976. Effects of some clearcutting practices on small-mammal populations in western Oregon. Northw. Sci. 50:189-208.

Johnson, D. R., and R. M. Hansen. 1969. Effects of range treatment with 2,4-D on rodent populations. J. Wildl. Manage. 33:125-132.

Klinka, K., F. C. Nuszdorfer, and L. Skoda. 1979. Biogeoclimatic Units of Central and Southern Vancouver Island, British Columbia. British Columbia Ministry of Forests, Victoria, British Columbia.

Leslie, P. H., and D. H. S. Davis. 1939. An attempt to determine the absolute number of rats in a given area. J. Anim. Ecol. 8:94-113.

Petticrew, B. G., and R. M. F. S. Sadlier. 1974. The ecology of the deer mouse *Peromyscus maniculatus* in a coastal conifer forest. I. Population dynamics. Can. J. Zool. 52:107-118.

Sadlier, R. M. S. F. 1974. The ecology of the deer mouse *Peromyscus maniculatus* in a coastal coniferous forest. II. Reproduction. Can. J. Zool. 52:119-131.

Sullivan, T. P., and D. S. Sullivan. 1982. Responses of a deer mouse population to a forest herbicide application: reproduction, growth, and survival. Can. J. Zool. 59:1148-1154.

Sutton, R. F. 1978. Glyphosate herbicide: an assessment of forestry potential. For. Chron. 54:24-28.

van Horne, B. 1981. Demography of *Peromyscus maniculatus* populations in seral stages of coastal coniferous forests in southeast Alaska. Can. J. Zool. 59:1045-1061.

von Schuckmann, S. 1986. The implications of brush control to wildlife and fish. Proc. Vegetation Management Symposium. Association of British Columbia Professional Foresters, Vancouver. Pp. 63-76.

Wahlgren, J. R. 1979. The effects of the herbicide Roundup® on reproduction in mice. University of British Columbia, Vancouver. B.S. Thesis.

Received 15 December 1986
Accepted for publication 6 April 1987

Honorary Life Members

Ewart M. Baldwin
Irven O. Buss
L. C. Cady
Charles D. Campbell
Robert L. Carr
Julian L. Culbertson
Rexford Daubenmire
Glenn Deitschman
R. A. Diettert
Bruce V. Ettling
William K. Ferrell
C. Clement French
Stanley P. Gessel
N. S. Golding
Phil Haddock
H. P. Hansen
Adolph Hecht
Kenneth Holmes
G. Brooks King
Rufus W. Kiser
Lewis and Clark High School Library (In memory of Thomas Large and J. G. McCracken)
Joseph W. Mills
Milton M. Mosher
Richard J. Naskali
Frank D. Nicol
Frances J. Schadegg
C. Gardner Shaw
Leona M. Sundquist
Oscar Sziklai
Robert F. Tarrant
Richard B. Walker
D. J. Wort

1987 Sustaining Institutional Members

Battelle Northwest, Richland, Washington
EG&G Idaho, Inc., Idaho Falls, Idaho
MacMillan Bloedel, Ltd., Nanaimo, British Columbia, Canada
Potlatch Corporation, Lewiston, Idaho
The Washington Water Power Company, Spokane, Washington
Weyerhaeuser Company, Centralia, Washington

1987 Institutional Members

Boise State University, Boise, Idaho
British Columbia Institute of Technology, Burnaby, British Columbia, Canada
Central Oregon Community College, Bend, Oregon
Central Washington University, Ellensburg, Washington
Centralia College, Centralia, Washington
College of Idaho, Caldwell, Idaho
Eastern Montana College, Billings, Montana
Eastern Oregon State College, LaGrande, Oregon
Eastern Washington University, Cheney, Washington
Edmonds Community College, Lynnwood, Washington
The Evergreen State College, Olympia, Washington
George Fox College, Newberg, Oregon
Grays Harbor College, Aberdeen, Washington
Green River Community College, Auburn, Washington
Highline Community College, Midway, Washington
Idaho State University, Pocatello, Idaho
Lewis-Clark State College, Lewiston, Idaho
Lewis and Clark College, Portland, Oregon
Linfield College, McMinnville, Oregon
Montana College of Mineral Science and Technology, Butte, Montana
Mt. Hood Community College, Gresham, Oregon
North Idaho College, Coeur d'Alene, Idaho
Northern Montana College, Havre, Montana
Pacific Lutheran University, Tacoma, Washington
Pacific University, Forest Grove, Oregon
Peninsula College, Port Angeles, Washington
Portland State University, Portland, Oregon
St. Martin's College, Lacey, Washington
Shoreline Community College, Seattle, Washington
Simon Fraser University, Burnaby, British Columbia, Canada
Skagit Valley College, Mount Vernon, Washington
Southern Oregon State College, Ashland, Oregon
Southwestern Oregon Community College, Coos Bay, Oregon
Spokane Falls Community College, Spokane, Washington
University of Alaska, Fairbanks, Alaska
University of Idaho, Moscow, Idaho
University of Montana, Missoula, Montana
University of Puget Sound, Tacoma, Washington
University of Victoria, British Columbia, Canada
University of Washington, Seattle, Washington
Walla Walla College, College Place, Washington
Washington State Library, Olympia, Washington
Washington State University, Pullman, Washington
Western Washington University, Bellingham, Washington
Whitman College, Walla Walla, Washington
Whitworth College, Spokane, Washington
Yakima Valley College, Yakima, Washington

1987 Sustaining Individual Members

Donald J. Brown, Richland, Washington
Randall E. Brown, Pasco, Washington
Nelsa M. Buckingham, Port Angeles, Washington
John H. Crow, Port Murray, New Jersey
Bruce Ettling, Vancouver, Washington
George R. Fahnestock, Seattle, Washington
William H. Funk, Pullman, Washington
Gerald H. Haddock, Wheaton, Illinois
Donald Hanley, Seattle, Washington
Charles R. Hatch, Moscow, Idaho
Mary M. Hektner, Arcata, California
Francis R. Herman, Fairbanks, Alaska
Richard K. Hermann, Corvallis, Oregon
Barry L. Keller, Pocatello, Idaho
Giles W. Maloof, Boise, Idaho
Emmett B. Moore, Jr., Richland, Washington
Howard R. Panik, Carson City, Nevada
William H. Rickard, Richland, Washington
Diane E. Robbins
Edward S. Schreiner, Port Angeles, Washington
Dale Stradling, Cheney, Washington
Robin J. Tausch, Reno, Nevada
Daniel W. Uresk, Rapid City, South Dakota
George H. Ward, Husum, Washington
Shepard M. Zedaker, Christiansburg, Virginia

Northwest Science

General Information

Publication in *Northwest Science* is open to scientists in the basic, applied, and social sciences who are engaged in original or fundamental research. *Northwest Science* does not publish notes, letters, or bibliographic papers. All submissions are reviewed by at least two referees and one associate editor. While submissions from outside the Pacific Northwest are welcome, at least one author of all papers considered for publication must be a member of the Northwest Scientific Association.

Information for Authors—A complete copy of the *Northwest Science* "Information for Authors" is available from the Editor.

Page Charges—Page charges are currently $60 per printed page. Petition for partial payment or waiver of these charges should be directed to the Editor upon the manuscript's being accepted for publication.

Manuscripts—Submit three copies of the paper (including tables and figures) to the Editor. Manuscripts should be typewritten on 8½x11 paper and *double-spaced throughout (including abstract, acknowledgments, literature cited, tables, and legends for figures);* provide ample margins. Avoid unnecessary footnotes. Do not break words at the end of a line. Format and style of manuscripts should conform to general usage in recent issues.

An abstract, written in complete sentences and not exceeding 250 words, should precede every article. It should succinctly state the objectives, the experimental design, the principal observations, and conclusions of the paper. Authors are reminded of the diverse disciplines and readership served by the journal; with this in mind, the abstract should conclude with a sentence or two stating the broader significance of the paper.

Literature citations should have the author's name and year of publication in the text; e.g. (Jones 1978). Citations should be double-spaced and listed in alphabetical order at the end of the article.

Present all data in international (SI) units. English equivalents may be added parenthetically. Use the 24-hour clock (0600 and 2300) and continental dating (17 November 1982).

Equations should be presented camera-ready. Symbols should be large enough to be legible after a ⅓ to ½ reduction in size, but not overly large.

Tables should be typewritten (double-spaced) separately from the text. Original art work or glossy prints of photographs must be submitted for reproduction. Art work and lettering should be large enough (but not overly large) to provide clarity after a 50 percent reduction in size for printing. The author's name and figure number should be penciled on the back of each illustration. Provide a scale for distance on map illustrations. Legends for illustrations should be typed (double-spaced) as a section of the manuscript; do not use a separate page for each legend.

Length of manuscripts is limited to 15 pages of printed copy. Two typed pages are approximately equal to one journal page.

Authors of Biological Papers—On first mention, a species should be designated by common name followed by systematic binomial. For abbreviations and forms of titles for serial publications, follow the *BIOSIS List of Serials.* Consult with the *Council of Biology Editors (CBE) Style Manual,* 4th ed., for general information on manuscript preparation.

Correspondence—Correspondence will be between senior author and the Editor.

Editing—In addition to being reviewed by two referees and an associate editor, manuscripts will be edited for grammatical correctness and clarity.

Galley Proofs and Reprints—One set of proofs will be sent to the senior author for correction shortly before publication; proofs should be returned to the Editor within three days of receipt. Senior authors should inform the Editor of any change of address for handling proofs. Reprints must be ordered when the proofs are returned. A schedule of reprint prices will be sent to the author with the proofs.

Non-Profit Org.
BULK RATE
U.S. POSTAGE
PAID
PULLMAN, WA
Permit No. 1

Northwest Science

Quarterly Publication of the Northwest Scientific Association

Papers published in *Northwest Science* are indexed in *Current Contents, Science Citation Index, Biological Abstracts, The Zoological Record, Recent Literature Supplement to The Auk, Abstracts in Anthropology, Bibliography and Index of Geology, Chemical Abstracts, Bibliography of Agriculture, Forestry Abstracts,* and *University Microfilms.*

Northwest Science is offered in exchange to other colleges, universities, learned societies, and libraries. Publications sent in exchange should be addressed to Washington State University Library, Technical Services Division, Pullman, Washington 99164-5610, U.S.A.

8489

November 1987 Volume 61, Number 4

NORTHWEST SCIENCE

CONTENTS

203 Composition and Structure of Oregon Ash (*Fraxinus latifolia*) Forest in William L. Finley National Wildlife Refuge, Oregon—**Robert E. Frenkel and Eric F. Heinitz, Lt. (j.g.)**

213 Winter Diet of the Harlequin Duck at Sequim Bay, Puget Sound, Washington—**William L. Gaines**

216 Age Estimates of Brook Trout from High-elevation Rocky Mountain Streams using Scales and Otoliths—**Steven J. Kozel and Wayne A. Hubert**

220 Roosevelt Elk Density in Old-Growth Forests of Olympic National Park—**D. B. Houston, B. B. Moorhead and R. W. Olson**

226 Bald Eagle Winter Abundance and Distribution in Eastern Washington—**Paul C. Fielder and Ronald G. Starkey**

233 Engelmann Spruce, Lodgepole Pine and Subalpine Fir Seed Germination Success on Ashbed Conditions—**P. M. Woodard and Grant Cummins**

239 Great Expectations; or Playing the Odds in the State Lotteries—**Sam C. Saunders and Michael E. Moody**

249 Evaluation of a Telemetry System for Measuring Habitat Usage in Mountainous Terrain—**Roland C. Kufeld, David C. Bowden and John M. Siperek, Jr.**

257 Habitat Characteristics of *Sidalcea nelsoniana* Piper (Malvaceae) at Walker Flat, Yamhill County, Oregon—**Judith B. Glad, Richard Mishaga and Richard R. Halse**

264 Features in the Early Development of Bull Trout (*Salvelinus confluentus*)—**William R. Gould**

Northwest Scientific Association

(Founded 1923)

The Northwest Scientific Association, an affiliate of the American Association for the Advancement of Science, is an association representative of the basic and applied sciences and of social sciences.

Membership in the Northwest Scientific Association, which includes a subscription to *Northwest Science,* is open to individuals for $14 per year ($8 per year for students). Institutional memberships, $40 per year. Sustaining membership, $25 per year for individuals and $100 per year for organizations, institutions, or agencies. Subscriptions are for the calendar year only.

Send change of address, payment of dues, or requests for undelivered issues to the Treasurer.

Editor of *Northwest Science*

Kenneth V. Kardong
Department of Zoology
Washington State University
Pullman, Washington 99164-4220

Officers of the Association

President Steven D. Tesch*
Oregon State University
Corvallis, Oregon (1989)

President-Elect W. H. Rickard
Pacific Northwest Laboratory
Richland, Washington (1990)

Secretary George H. Fahnestock
Seattle, Washington (1990)

Treasurer Robert K. Moseley
The Nature Conservancy
1221 South Main Street
Moscow, Idaho 83843 (1989)

Past President Donald Hanley
Washington State University
c/o University of Washington
Seattle, Washington (1988)

Trustees:

Robert Antibus
University of Montana
Missoula, Montana (1988)

Steven Benham
Pacific Lutheran University
Tacoma, Washington (1988)

Dan L. Campbell
United States Dept. of Agriculture
Olympia, Washington (1990)

Robert L. Carr
Eastern Washington University
Cheney, Washington (1990)

Richard A. Cellarius
Evergreen State College
Olympia, Washington (1988)

Wilbert R. Danner
University of British Columbia
Vancouver, B.C. (1989)

Kenneth Hammond
Central Washington University
Ellensburg, Washington (1989)

David Hansen
Pacific Lutheran University
Tacoma, Washington (1990)

Larry Larson
Oregon State University
Corvallis, Oregon (1988)

William Lopushinsky
U.S. Forest Service
Wenatchee, Washington (1990)

Gilbert B. Pauley
University of Washington
Seattle, Washington (1989)

William R. Rayburn
Washington State University
Pullman, Washington (1989)

W. H. Rickard
Pacific Northwest Laboratory
Richland, Washington (1988)

Harry Smith
University of British Columbia
Vancouver, B.C. (1988)

Steven D. Tesch
Oregon State University
Corvallis, Oregon (1988)

David H. Wagner
University of Oregon
Eugene, Oregon (1989)

H. Clare Wiser
Washington State University
Pullman, Washington (1990)

*Term of office expires in the year given in parentheses.

November 1987 Volume 61, Number 4

NORTHWEST SCIENCE

Editor	Kenneth V. Kardong	Washington State University
Managing Editor	Fred Bohm	Washington State University
Indexer	Caroline Hooper	
Associate Editors		
Aquatic Biology	Gary L. Larson	U.S. National Park Service/ Oregon State University
Botany	Suzanne M. Schwab	Eastern Washington University
Chemistry and Physics	Frank L. Curzon	University of British Columbia
Engineering and Mathematics	Gary L. Sheldon	Washington State University
Forestry	James K. Agee	U.S. National Park Service/ University of Washington
Geology	Franklin F. Foit, Jr.	Washington State University
Social Sciences	Philip D. Young	University of Oregon
Soils	Robert L. Edmonds	University of Washington
Wildlife Biology	Margaret A. O'Connell	Washington State University
Zoology	Kerry Paul Reese	University of Idaho

CONTENTS

203 Composition and Structure of Oregon Ash (*Fraxinus latifolia*) Forest in William L. Finley National Wildlife Refuge, Oregon—**Robert E. Frenkel and Eric F. Heinitz, Lt. (j.g.)**

213 Winter Diet of the Harlequin Duck at Sequim Bay, Puget Sound, Washington—**William L. Gaines**

216 Age Estimates of Brook Trout from High-elevation Rocky Mountain Streams using Scales and Otoliths—**Steven J. Kozel and Wayne A. Hubert**

220 Roosevelt Elk Density in Old-Growth Forests of Olympic National Park—**D. B. Houston, B. B. Moorhead and R. W. Olson**

226 Bald Eagle Winter Abundance and Distribution in Eastern Washington—**Paul C. Fielder and Ronald G. Starkey**

233 Engelmann Spruce, Lodgepole Pine and Subalpine Fir Seed Germination Success on Ashbed Conditions—**P. M. Woodard and Grant Cummins**

239 Great Expectations; or Playing the Odds in the State Lotteries—**Sam C. Saunders and Michael E. Moody**

249 Evaluation of a Telemetry System for Measuring Habitat Usage in Mountainous Terrain—**Roland C. Kufeld, David C. Bowden and John M. Siperek, Jr.**

257 Habitat Characteristics of *Sidalcea nelsoniana* Piper (Malvaceae) at Walker Flat, Yamhill County, Oregon—**Judith B. Glad, Richard Mishaga and Richard R. Halse**

264 Features in the Early Development of Bull Trout (*Salvelinus confluentus*)—**William R. Gould**

Upcoming Meetings of the Northwest Scientific Association

The 1988 spring meeting of the Northwest Scientific Association (NWSA) will be held March 23-26, 1988, on the campus of Southern Oregon State College (SOSC), Ashland, Oregon. Dr. Claude Curran, Director of the School of Social Science, is the general program chairman. He will be sending to each member more specific information. The meeting will be co-sponsored by the Oregon State University Forestry Intensified Research (FIR) Program, a major cooperative research venture that will be celebrating ten years of reforestation research in southern Oregon.

Southern Oregon promises to be a special place to spend a spring vacation, despite the travel distance involved for many of you. Plan to bring the family and spend the entire week! Ashland should be a warm and sunny break for those of you coming from colder climates. Ashland also offers some excellent cultural entertainment. The world-famous Oregon Shakespearean Festival will be underway and tickets should be more readily available in March than during summer months. If this is your first trip to Ashland, at least one play is a must!

Southern Oregon offers a rich and diverse environment for field study and vacationing. The Kalamath and Cascade Mountains offer tremendous plant, animal, and geological diversity. Crater Lake National Park, Lava Beds National Monument, Oregon Caves National Monument, Redwood National Park, the wild and scenic Rogue River, and the rugged Pacific Ocean coastline are all within a day's drive of the SOSC campus.

For those interested in forest management, southern Oregon offers an array of management practices and challenges. The FIR Program will highlight the meetings with a one-day symposium that summarizes reforestation research directed at site conditions with steep, rocky soils, aggressive competing vegetation, and hot, dry summers.

For students attending this year's meeting, two recent changes will be of interest. *Student members* of the NWSA *presenting* a paper will have their registration fee waived. Also, abstracts of all papers presented at the meeting will be formally published as a supplemental issue of *Northwest Science.* This provides a legitimate citation for resumes and also ensures better distribution of research results to libraries and other colleagues. The annual meeting continues to be an excellent place for students to present results of their research and we hope faculty will encourage them to participate.

Call for Applications to the Student Research Grants Award Committee

Research grants in the amount of $300 shall again be awarded to students with successful candidates announced at the spring meeting of the Northwest Scientific Association. Application forms should be returned to the Chairman of the Research Grants Committee no later than 15 February 1988. For further information and application forms write to:

Dr. William H. Rickard, Chairman
Battelle-Northwest Laboratories, Box 999
Richland, Washington 99352

Call for Nominations

Nominations for President-Elect, Treasurer, and seven Trustee positions should be mailed by 15 February 1988 to:

Dr. Kenneth Hammond
Department of Geography
Central Washington University
Ellensburg, Washington 98926

Nominations for Outstanding Northwest Scientist or for Honorary Life Member should be mailed by 15 February 1988 to:

Dr. Gilbert B. Pauley
Department of Fisheries
University of Washington
Seattle, Washington 98195

Robert E. Frenkel, Department of Geography,
Oregon State University, Corvallis, Oregon 97331

and

Eric F. Heinitz, Lt. (j.g.), U.S. Coast Guard, Marine Inspection Office,
Battery Park Building, New York, New York 10004

Composition and Structure of Oregon Ash (*Fraxinus latifolia*) Forest in William L. Finley National Wildlife Refuge, Oregon

Abstract

We describe two Oregon ash (*Fraxinus latifolia*) plant communities at William L. Finley National Wildlife Refuge in the central Willamette Valley which differ in habitat, composition, and structure. The *Fraxinus latifolia/Carex obnupta* community type, with many young trees (average core age 59 years) of small diameter (average 14 cm dbh), has an open understory of scattered *C. obnupta* patches and occupies moist overflow sites. The more floristically rich *Fraxinus latifolia/Symphoricarpos albus* community type, with large diameter (average 20 cm dbh) and older trees (average core age 72 years), has a thick shrub understory and occupies better drained, but still moist, sites. Both forest community types are young; however, the *C. obnupta* community has recently expanded into former wet prairie with cessation of aboriginal burning and historic grazing.

Introduction

Oregon ash (*Fraxinus latifolia* Benth.) ranges from northern Washington to the San Bernardino Mountains, California. Forests dominated by Oregon ash are particularly well developed in the interior valleys of western Oregon where the species occupies riparian strips and adjacent poorly drained bottom lands. Associated moist site trees are *Acer macrophyllum, Alnus rubra, Populus trichocarpa,* and *Salix* spp., while *Abies grandis, Pseudotsuga menziesii,* and *Quercus garryana* may be present on drier sites (Franklin and Dyrness 1973, Owston in press). Although seldom extensive, *Fraxinus* forests are prominent landscape features, providing a major forest component to riparian habitat and benefitting fish, wildlife, and recreational resources (Frenkel *et al.* 1985). Surprisingly, characteristics of these forests have not previously been examined.

A modified maritime climate prevails over the Willamette Valley with wet, mild winters and warm, relatively dry summers, and a slight rain shadow effect. Representative climatic data, following the standardized system of Walter and Lieth (1967), are summarized in Figure 1 for Hyslop Agronomy Farm, Corvallis. Based on precipitation and temperature criteria, surplus moisture occurs from September to June. In riparian and bottom land habitats typically occupied by *Fraxinus,* this surplus is accentuated by seasonal flooding from December to April and by high water tables in early summer. Potential anaerobic conditions may occur as suggested by gleying in soil profiles. A brief drought period ensues during the summer months when soils may desiccate for short periods; but, extensive drought is not present.

Soils of central Willamette Valley *Fraxinus* forests are most commonly grouped in the Waldo-Bashaw association, poorly drained silty clay loams and clays. The principal soil series related to the Refuge ash forests is Bashaw silty clay, a deep, poorly drained soil with montmorillonite clays classified as a Typic Pelloxerert. The black, heavy, silty clay loam surface layer reaches depths of between 25 and 40 cm. Underlying horizons are black to very dark gray with a layer of silty clay above clay. When wet, the soil becomes very sticky and plastic. Upon drying it cracks and becomes very hard (Knezevich 1975).

One of the best examples of Oregon ash forest is in William L. Finley National Wildlife Refuge, 16 km south of Corvallis in the central Willamette Valley, where *Fraxinus* spans a strip approximately 400 m wide adjacent to Muddy Creek and Gray Creek and nearby shallow swales and overflow lands (Figure 2). The trees are thickly draped by foliose lichens *Evernia prunastri* (L.) Ach., *Ramalina menziesii* Tayl., *Usnea ceratina* Ach., and *U. subfloridana* reflecting moist atmospheric conditions.

Vegetation in the Refuge is typical of the interior valleys of western Oregon (Franklin and Dyrness 1973); several physiognomic types

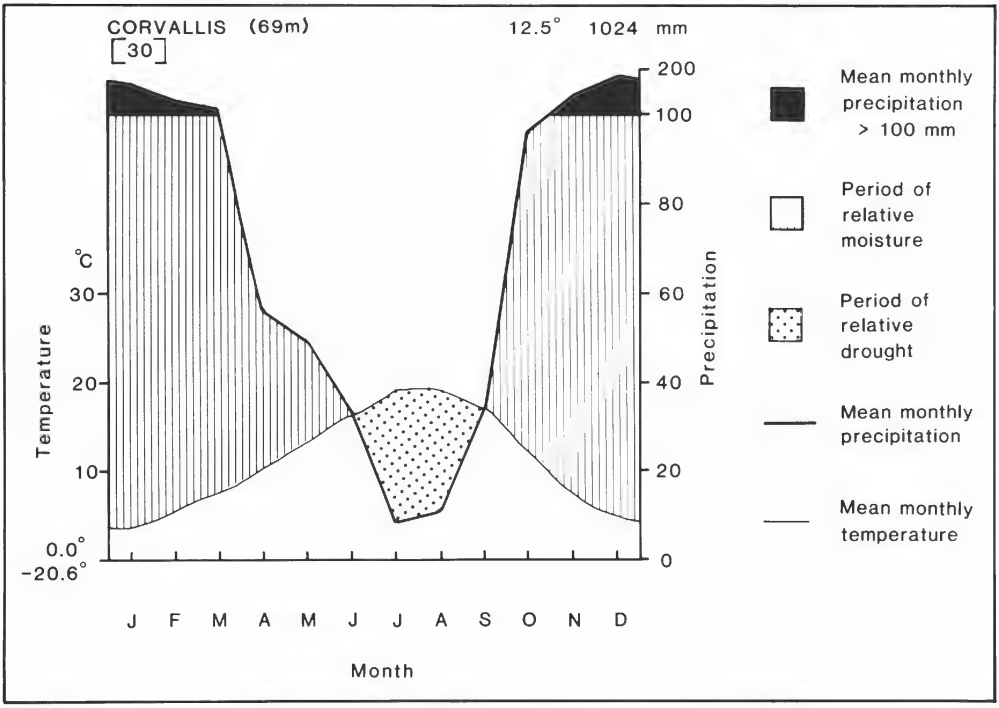

Figure 1. Climograph for Hyslop Agronomy Farm, Corvallis, Oregon, following the standardized Walter and Lieth system.

mapped by Exler (1982) are generalized in Figure 2. Oak woodland, dominated by *Quercus garryana,* has been described and classified by Thilenius (1968) and is the closest of these types in structure and composition to the ash forest. Thilenius identified four oak community types in the interior valleys of western Oregon which, in order of increasing moisture, are: *Rhus diversiloba; Amelanchier alnifolia/Symphoricarpos albus; Prunus avium/Symphoricarpos albus;* and *Corylus cornuta* var. *californica/Polystichum munitum.* All are regarded as seral and occupy well drained slopes and ridges.

Wet prairie, maintained as grassland by historic fire and grazing, is also considered seral, but to *Fraxinus* forest (Moir and Mika 1972, Franklin and Dyrness 1973, Towle 1982, Marshall 1985). These heavily disturbed prairies, dominated by *Deschampsia caespitosa, Hordeum brachyantherum* and *Carex* spp., contain many alien species and bear little structural resemblance to ash forest.

The *Fraxinus latifolia* forest is transitional in moisture status between oak woodland and wet prairie. Prior to early settlement, *Fraxinus* forests fringed almost all water courses in the Willamette Valley. The General Lands Office township and range survey conducted in the Refuge area in 1853, documents a 100 m wide strip of *Fraxinus* forest along Muddy Creek. Survey notes and plat maps are available and were examined at the Oregon State Office of the Bureau of Land Management. Additionally, historic accounts of the Refuge area and old aerial and ground photographs show many of the present stands more limited in extent than present. Aboriginal burning apparently kept *Fraxinus* from expanding into prairie (Habeck 1961, Johannessen *et al.* 1971, Towle 1982). In the late-19th century, intense grazing by livestock replaced fire as a dominant influence in the Refuge area (Towle 1982). Gradually, grazing intensity diminished and, in the early 1960's, ceased altogether (personal communication John Cornely, Refuge Biologist).

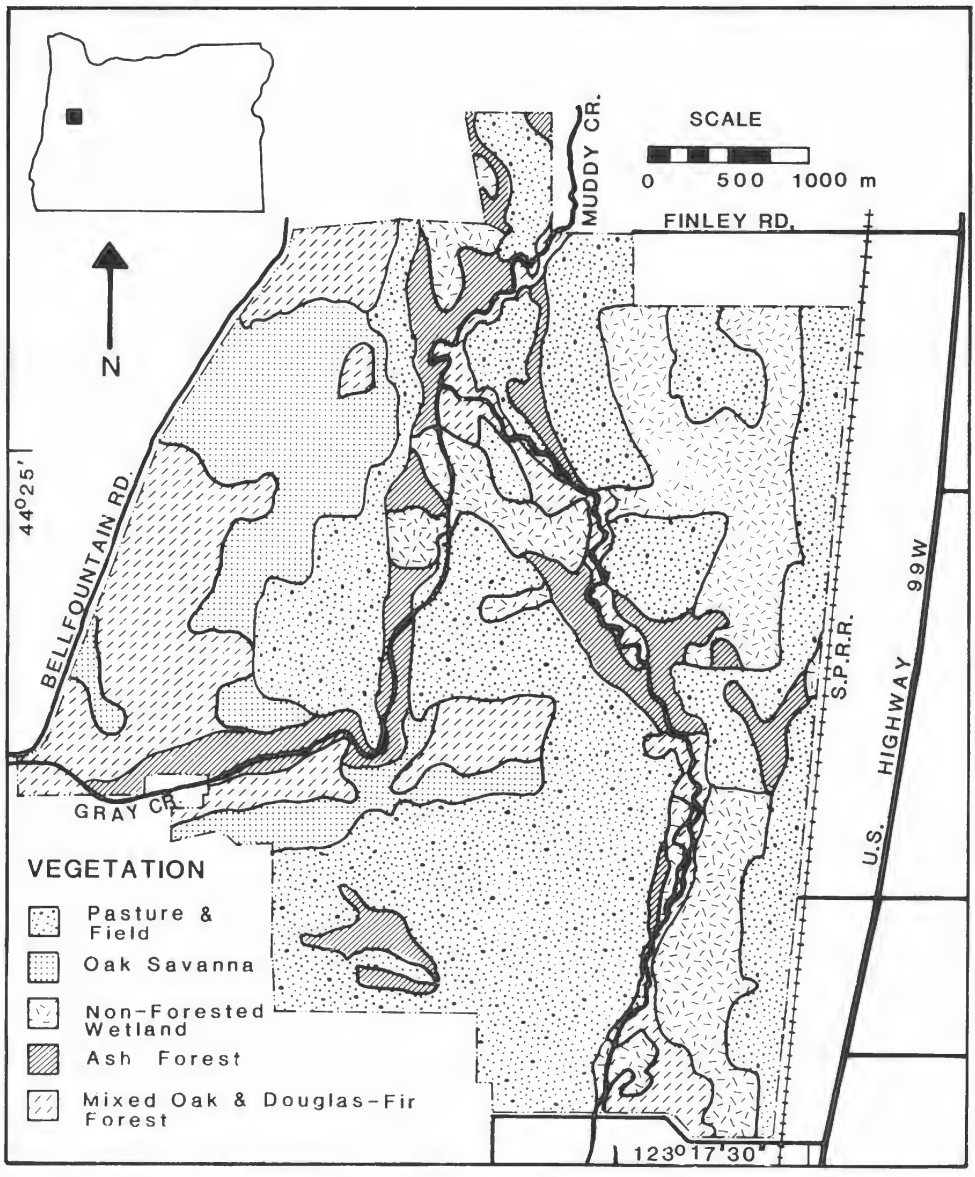

Figure 2. Vegetation of W. L. Finley National Wildlife Refuge generalized after Exler (1982) and location in Oregon.

Unchecked by fire and cattle, ash invaded prairie, setting the stage for the present vegetation.

The questions addressed in this paper are based on the above relationships: (1) What are the structure and composition of *Fraxinus* forests in the Finley Refuge? (2) How does the distribution of *Fraxinus* forests relate to the moisture gradient? (3) What is the relationship between

Fraxinus forests and *Quercus* forests? (4) How does the present distribution reflect historic practices of burning and grazing?

METHODS

To gain familiarity with the range in composition and structure of ash forests, a general survey of *Fraxinus* forest distribution was first conducted throughout the Willamette Valley. In 1982, 19 stands were selected in the W. L. Finley National Wildlife Refuge based on their relative homogeneity in habitat, composition, structure, and adequacy of stand size. Because of its accessibility and extent, one additional stand was located at The Nature Conservancy Cogswell-Foster Preserve, 19 km southeast of the Refuge.

Circular, 12.6 m radius macroplots of 500 m^2 were located randomly within selected stands, one macroplot per stand, and the following data recorded for live and dead trees: total percent canopy cover; percent canopy cover by species; diameter at breast height (dbh) of all trees by species >5 cm dbh; number of "reproductive" stems per macroplot (stems <5 cm dbh); number and dbh of downed dead wood >5 cm dbh; vigor class (vigorous, impaired, dead); and height and increment core-age of two-to-four of the largest diameter ash trees in each macroplot. Core-ages were determined in the field with the aid of hand lens. Only in a few cases were multiple cores taken from the same tree. Understory composition was recorded from 12, one m^2 microplots placed at four, seven, and ten meter intervals along four transects set in cardinal directions within the macroplot. Cover was estimated for each species by Daubenmire (1959) canopy cover classes. Taxonomy and nomenclature follow Hitchcock and Cronquist (1973). We use the term 'community' to define a general assemblage of plants and 'community type' or 'type' for the abstract classificatory unit comparable to the plant association.

Prior to analysis, mean percent cover was transformed to octave values (Gauch 1982). Floristic data were used to classify macroplots into community types with the aid of several multivariate programs including: TABORD, which structures phytosociological data in the form of an association table based on sample similarity (Maarel *et al.* 1978); CLUSTER, a polythetic agglomerative clustering program using a Bray-Curtis dissimilarity measure and a flexible fusion strategy, $B = -0.25$ (Boesch 1977, Keniston 1978); and TWINSPAN, an iterative polythetic divisive technique based on reciprocal averaging (Hill 1979a). Additionally, we analyzed floristic data with DECORANA, an ordination achieved by detrended correspondence analysis (Hill 1979b). Within-community similarity was determined by an abundance-weighted similarity ratio (Maarel *et al.* 1978).

Species diversity was analyzed by PRHILL, an unpublished computer program developed by B. G. Smith that calculates jackknife estimates of M. O. Hill's diversity numbers (Hill 1973, Alatalo 1981, Heltsche and Forrester 1983) for each community type. By simulation, Heltsche and Forrester have shown that jackknife estimates of diversity permit comparison of communities under a wide variety of plot sizes. Four measures of diversity are displayed: mean number of species per macroplot; expected total number of species in a community type (N_0); inverse of Simpson's diversity index (N_2); and M. O. Hill's evenness ratio (N_2/N_1).

Tree diameter data were grouped in 5 cm diameter classes and plotted by frequency histograms for each macroplot and subsequently aggregated by community type. Basal area and density were determined from measured trees in each plot. An age-size relationship, calculated from 60 trees, was used to characterize the age structure of plant community types. A variety of average community characteristics were assessed with Student's t-test in which significance was judged at $p = 0.05$.

RESULTS

Plant Communities

The *Fraxinus latifolia/Carex obnupta* and the *Fraxinus latifolia/Symphoricarpos albus* community types are identified based on floristic classification (Table 1 and Figure 3). Both community types show a relatively low level of within-community similarity, averaging 61 percent (Table 2). This heterogeneity is further demonstrated by spread-out plot distribution in the ordination (Figure 4), the types being distinguished more by differences in species abundance than by species presence-absence. Since classifications based on TABORD and CLUSTER were in close agreement, only the CLUSTER classification is

TABLE 1. Percent constancy and mean percent cover in *Fraxinus latifolia* community types. Only species with at least two percent cover in a community type are included.

Stratum and Species	Community Type: *Fraxinus latifolia/ Carex obnupta* (n=9) const./mean cov.	Community Type: *Fraxinus latifolia/ Symphoricarpos albus* (n=11) const./mean cov.
TREES		
Fraxinus latifolia	100/84	100/80
Quercus garryana	—	27/ 6
SHRUBS		
Crataegus douglasii	56/ T	27/ 4
Spiraea douglasii	44/ 2	36/ 2
Rubus ursinus	33/ T	91/22
Rosa eglanteria	33/ T	64/ 6
Symphoricarpos albus	22/ T	82/26
Lonicera involucrata	—	18/ 3
HERBS		
Carex obnupta	89/36	45/10
Galium trifidum	89/ 2	64/ 4
Carex deweyana	78/ 4	73/10
Eleocharis acicularis	67/ 4	55/ 2
Ranunculus uncinatus	67/ 2	100/ 4
Stellaria calycantha	56/ T	82/ 4
Oenanthe sarmentosa	33/12	27/ 3
Elymus glaucus	33/ 4	45/ 1
Carex unilateralis	33/ 3	45/ 8
Carex leporina	33/ 2	18/ T
Veronica scutellata	33/ T	55/ 2
Montia sibirica	22/ T	64/14
Tellima grandiflora	22/ T	55/ 4
Stachys cooleyae	22/ T	27/ 3
Myosotis laxa	22/ T	9/ 2
Geum macrophyllum	11/ T	82/ 3
Agrostis tenuis	11/ T	64/ 5
Galium aparine	11/ T	64/ 4
Polysticum munitum	—	55/ 4
Perideridia gairdneri	—	55/ 3

TABLE 2. Selected floristic characteristics of *Fraxinus latifolia* community types.[a]

Characteristic	Community Type: *Carex obnupta* (n=9)	Community Type: *Symphoricarpos albus* (n=11)
Within-Community Similarity (%)	66.1	56.8
Mean No. Species per Macroplot	13.7	22.5
Total No. Species Expected in Type (N_0)	50.8 s.e.=3.2	66.9 s.e.=4.2
Inverse of Simpson's Diversity Index (N_2)	14.7 s.e.=1.6	32.9 s.e.=2.5
Evenness Index $\frac{(N_2)}{(N_1)}$	0.525	0.743

[a]Within-community similarity is based on an abundance-weighted similarity ratio (Maarel *et al.* 1978). Diversity indexes are based on PRHILL (see methods).

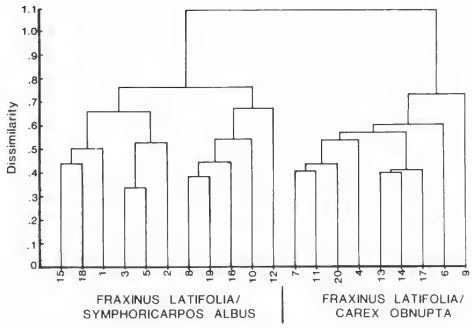

Figure 3. Cluster dendrogram based on CLUSTER (Keniston 1978) using the Bray-Curtis dissimilarity index and flexible clustering strategy, $B = -0.25$.

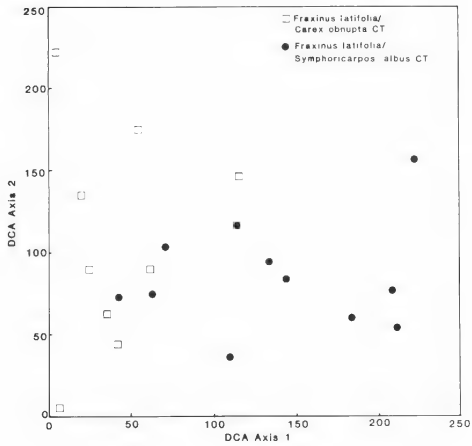

Figure 4. Detrended correspondence analysis ordination of W. L. Finley National Wildlife Refuge *Fraxinus latifolia* macroplots. CLUSTER and TABORD community classification is superimposed by symbol.

displayed. Several floristically different macroplots were classified differently by TWINSPAN when compared to the TABORD and CLUSTER classifications.

The *Fraxinus latifolia/Carex obnupta* community type is marked by low shrub cover (3%) and high cover and constancy of *Carex obnupta.* Other common species include *C. deweyana, Eleocharis acicularis,* and *Galium trifidum* (Table 1). *Carex obnupta* typically grows in dense patches ranging in size from one to several square meters and exhibits total macroplot cover often in excess of 60 percent. Bare ground is usually conspicuous, averaging 23 percent of the plot area (Table 3). Species richness is lower than in the *Symphoricarpos albus* type, averaging 13.7 species per macroplot (Table 2). The jackknife estimate of community richness, or total number of species expected in a community type, is 50.8 species and is less than in the *S. albus* type. The inverse of Simpson's diversity index is 14.7 and evenness index is 0.525 suggesting a relatively simple community with high dominance by a few species. The *Fraxinus* overstory canopy is commonly closed, reducing summer insolation at ground level. Although no measurements were made, we observed extended periods of spring flooding, depressed topography, and soils with high clay content and low permeability. This community type is usually situated away from main water courses in overflow lands.

The *Fraxinus latifolia/Symphoricarpos albus* community type has a prominent shrub cover (Tables 1 and 3) with *Symphoricarpos albus, Rubus ursinus,* and *Rosa eglanteria* having high constancy and/or cover (Table 1). Characteristic herbs with high constancy or cover include *Ranunculus uncinatus, Stellaria calycantha, Montia sibirica,* and *Galium aparine* (Table 1). *Quercus garryana* occurs in three plots as a codominant. The *S. albus* community type, with a within-type similarity of 57 percent (Table 2), is less floristically homogeneous than the *C. obnupta* type (within-type similarity 66%). Mean species richness per macroplot is 22.5 species. A jackknife community richness estimate of 66.9 species suggests a richer type than the *C. obnupta* type and the inverse of Simpson's diversity index of 32.9 and an evenness index of 0.737 indicates that dominance is shared by several species and there is more evenness in species abundance than in the *C. obnupta* community. The *S. albus* community, with a more open canopy and less flooding than the *C. obnupta* community, has a mean bare ground cover per plot of 2 percent (Table 3). The *S. albus* community often occupies natural levees adjacent to streams and margins of the ash forest where it abuts agricultural fields. Both locations are associated with somewhat coarser textured soils.

Fraxinus forest plots are ordinated by detrended correspondence analysis (DCA) yielding four eigenvalues (0.34, 0.17, 0.09, 0.05). The principal two ordination axes are displayed in Figure 4 together with the superimposed

TABLE 3. Selected structural characteristics of *Fraxinus latifolia* plant community types.

Characteristic	Community Type *Carex obnupta* (n=9)	Community Type *Symphoricarpos albus* (n=11)	t[a]	
Mean Total Tree Cover (%)	83.9	79.4	1.66	
Mean Total Shrub Cover (%)	3.1	70.5	4.01	*
Mean Bare Ground (%)	22.6	2.4	3.51	*
Mean Litter (%)	53.8	67.9	1.80	
Mean No. Down Dead Trees (ha^{-1})	218	136	1.37	
Mean Dens. Total Trees (ha^{-1})	2446	1358	3.46	*
Mean Dens. Live Trees (ha^{-1})	1824	1012	3.44	*
Mean Dens. Vigorous Trees (ha^{-1})	1484	848	3.19	*
Mean Dens. Dying/Dead Trees (ha^{-1})	962	511	3.01	*
Mean Dens. Stand. Dead Trees (ha^{-1})	626	346	2.38	*
Mean Dens. Reprod. Stems (ha^{-1})	2274	854	2.98	*
Mean Stem Diameter (cm)	14.1	19.7	1.96	
Mean Stand Basal Area (m^2 ha^{-1})	32.2	31.4	0.25	
Mean *Fraxinus* Core Age (yrs)	59.3	72.2	3.52	*

[a]* indicates significance at p=0.05

TABORD and CLUSTER community classification. Lacking quantitative environmental measurements, it is difficult to interpret these axes. Plots in the *Carex obnupta* community type are on the left of the ordination and *Symphoricarpos* community type plots on the right. The principal axis (DCA axis 1) may indicate persistence of moisture. *Symphoricarpos albus* stands are associated with drier and more coarse textured soils characteristic of natural levees and gently sloping margins of bottomlands. Figure 5 shows a relatively weak positive relation (r=0.53, p=0.020) between ash core-age and DCA axis 1 score, suggesting correspondence between older ash stands and assumed drier sites.

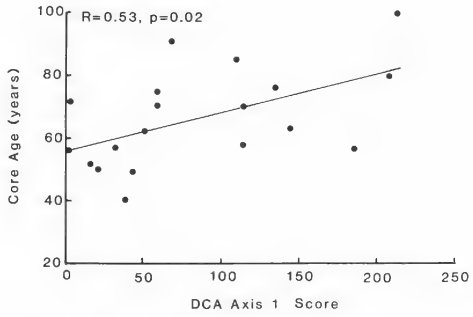

Figure 5. Relation between detrended correspondence analysis ordination principal axis score (DCA Axis 1) and core age of largest *Fraxinus* trees in each macroplot.

Structure

The two community types are distinct in tree diameter, density, number of "reproductive stems," and size structure (Table 3 and Figure 6). The *Fraxinus latifolia/Carex obnupta* community type exhibits many trees less than 15 cm dbh, few trees greater than 30 cm dbh, and a moderate number of standing dead trees 5-15 cm dbh. This structural pattern is shown in Figure 6 aggregated for all nine *Carex* community type plots. Mean total tree density is 2446 ha^{-1}. Although the proportion of vigorous to impaired to dead trees remains about the same in the two communities (about 61:13:26 respectively), there are more standing dead and down trees in the *Carex* type than in the *Symphoricarpos* type. The *Carex* plots also have a large number of reproductive stems (a mean of 2274 stems ha^{-1}).

The 11 plots allocated to the *Fraxinus latifolia/Symphoricarpos albus* community type, on the other hand, exhibit a more even distribution of stem diameters, fewer trees with diameters less than 5 cm dbh, a larger number of trees exceeding 30 cm dbh (Figure 6), a slightly more open canopy, and a fewer standing impaired and

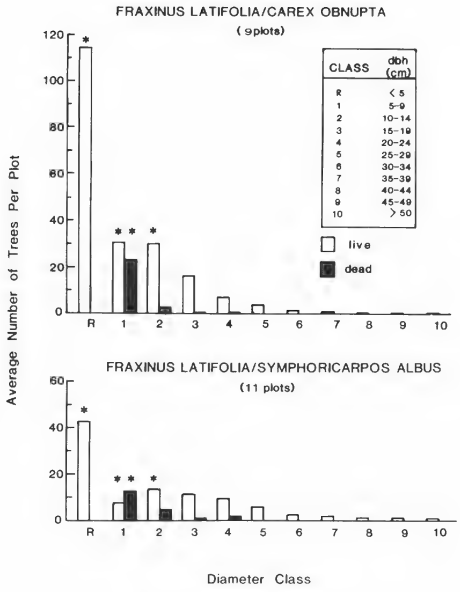

Figure 6. Tree size distribution in *Fraxinus latifolia/Carex obnupta* and *Fraxinus latifolia/Symphoricarpos albus* plant community types. Asterisk (*) indicates significantly different (p = 0.05) size class between the two communities.

dead trees than are present in the *C. obnupta* community type (Table 3). A total density of 1358 ha − 1 is significantly less than the density of the *C. obnupta* community. Although the two communities are structurally distinct, community basal area, reflecting both diameter and density, is not significantly different, 32.2 m2 ha − 1 for the *Carex* and 31.4 m2 ha − 1 for the *Symphoricarpos* community.

Coring ash trees is extremely difficult because of the toughness of the wood; furthermore, trees older than 100 years frequently had rotted centers and could not be aged. Because of these problems, only two-to-four of the largest, and presumably oldest, ash trees in each plot were cored. Age sampling was not representative of the total forest age structure. A weak positive relation exists between age and diameter for all plots ($r = 0.49$, $p = 0.000$). There is a somewhat stronger age-diameter relationship for the *Carex* plots ($r = 0.60$, $p = 0.0000$) than for the *Symphoricarpos* plots ($r = 0.47$, $p = 0.010$). The *Carex* communities with a mean core age of 59.3 years for the oldest ash trees, are significantly younger than the *Symphoricarpos* communities with a mean core age of at least 72.2 years. Because of the difficulty in aging trees older than 100 years, the relationships presented above are conservative; in other words, the distinction based on age between community types is at least as great as presented.

Discussion

The vegetation mosaic in the Willamette Valley, consisting of prairie, deciduous forest, and evergreen forest, has been heavily modified by man, both historically and presently (Johannessen *et al.* 1971, Towle 1982). Published studies of these types are few and their characteristics, environmental and successional relationships are only provisionally known (Franklin and Dyrness 1973). Both temporal and environmental gradients are evident. Temporally, wet prairie succeeds to deciduous *Fraxinus* forest on poorly drained moist sites (Moir and Mika 1972, Marshall 1985). Furthermore, following disturbance, dry sites are occupied serally by dry prairie, deciduous *Quercus garryana* forest, and ultimately by *Pseudotsuga menziesii* forest—a somewhat indeterminant successional sequence (Sprague and Hansen 1946, Franklin and Dyrness 1973). Environmentally, a moisture gradient may also be recognized in which the sequence with decreasing moisture is marsh, wet prairie, *Fraxinus* forest, *Quercus* forest (Boss 1983, Moir and Mika 1972, Thilenius 1968). In the Willamette Valley, ash forest appears to have a terminal position along the seral gradient and a central position along the moisture gradient. Our study of the composition and structure of *Fraxinus latifolia* forest in the Finley Refuge relates this moist forest type to these two gradients.

With respect to the moisture gradient, central Willamette Valley ash communities are assumed to respond to differences in inundation and drainage. Of the two identified community types, the *Carex obnupta* type occupies poorly drained bottom lands, is dense, and exhibits strong dominance by small diameter and relatively young *Fraxinus* trees. The *Symphoricarpos albus* type is found on natural levees and gentle slopes adjacent to overflow areas, is more open, and is dominated by larger and older *Fraxinus* trees than in the *Carex* type. Lower species diversity

and higher dominance in the *Carex* type than in the *Symphoricarpos* type agrees with observations that overflow areas have greater anaerobic conditions leading to stressed vascular plants (Lee *et al.* 1985).

Compositionally, the *Fraxinus* community types were heterogeneous and shared many species. These types occupy habitats intermediate in moisture status between drier *Quercus garryana* forest sites (Thilenius 1968) and more hydric wet prairie and palustrine marsh sites (Moir and Mika 1972, Marshall 1985, Boss 1983). Understory composition of the more mesic *Quercus garryana* communities shows some, but not close, resemblance to the *Symphoricarpos albus* community type. The lack of similarity is probably because a full range of intermediate stands between those examined by Thilenius (1968) and those reported upon here were not sampled. Likewise, ash stands share many species with nearby wet prairies, including *Spiraea douglasii, Crataegus douglasii, Rosa eglanteria, Eleocharis acicularis,* and *Carex unilateralis.*

With respect to a seral gradient, ash forest appears to have a terminal position. *Fraxinus latifolia* is the major reproducing tree in each community. A dioecious species, *F. latifolia* is a prolific seeder in open stands but reproductively more limited in closed stands. Stump sprouts are common, especially where stems have been damaged (Owston in press). Ash is recognized as intolerant to moderately tolerant of shade, yet the distribution of *Fraxinus* throughout all size classes in both community types suggests a multiple age canopy with self replacement. Detailed age structure, however, was not examined. The relatively young age and high density of the *Fraxinus latifolia/Carex obnupta* community type suggests recent occupancy of the sites. There was no evidence of cut stumps or rotting logs. The more open and older *Symphoricarpos* type, with several ash trees in excess of 100 years and large diameter woody debris, indicates greater stand age but still stability in dominance, since *Fraxinus* continues to dominate both reproduction and overstory canopy.

As recently as 70 years ago, the ash forest in the Refuge area was limited to the immediate riparian strip of Muddy and Gray Greek. In combination, burning and grazing historically restricted the ash forest to a narrow riparian forest along natural levees within which *Quercus garryana* also flourished (Habeck 1961, Johannessen *et al.* 1971). The *Fraxinus latifolia/Symphoricarpos albus* type along the Muddy Creek today represents historic continuity with the earlier forested riparian strip. The present *Carex* community type, representing more recent encroachment into prairie, does not appear to have this historic continuity.

Floristic and structural analysis of *Fraxinus latifolia* forest in William L. Finley National Wildlife Refuge sheds light on history of the ash forest in the central Willamette Valley and its position with respect to temporal and environmental gradients. The present extensive ash forest on moist sites in the Refuge area is a relatively recent feature resulting from succession following the cessation of burning and grazing.

Acknowledgments

We wish to thank Palmer Sekora, Refuge Complex Manager, and John Cornely, Biologist at William L. Finley National Wildlife Refuge, for their logistic assistance throughout this project. Sherry Pittman identified lichen specimens for which we are grateful. Particular thanks are extended to Bradley G. Smith who provided program PRHILL for an analysis of diversity and many good suggestions for the paper. We also appreciate readings by Diana Bodker and Charles Halpern. We are especially thankful for many constructive and helpful suggestions from two anonymous and very dedicated reviewers.

Literature Cited

Alatalo, R. V. 1981. Problems in the measurement of evenness in ecology. Oikos 37:199-204.

Boesch, D. F. 1977. Application of numerical classification in ecological investigations of water pollution. Virg. Inst. Marine Sci. Spec. Sci. Rep. 77. EPA, Environ. Res. Center, Corvallis, Oregon.

Boss, T. R. 1983. Vegetation ecology and net primary productivity of selected freshwater wetlands in Oregon. Oregon State University, Corvallis. Ph.D. Dissertation.

Daubenmire, R. F. 1959. A canopy-coverage method of vegetation analysis. Northw. Sci. 33:43-66.

Exler, R. 1982. William L. Finley National Wildlife Refuge Vegetation. A color map designed by the Cartographic Service, Dept. Geogr., Oregon State University, Corvallis.

Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8, Pacific Northw. For. Range Exp. Sta., Portland, Oregon.

Frenkel, R. E., S. N. Wickramaratne, and E. F. Heinitz. 1985. Vegetation and Land Cover Change in the Willamette River Greenway in Benton and Linn Counties, Oregon: 1972-1981. Yearbook Assoc. Pacific Coast Geogr. 46:63-77.

Gauch, H. G., Jr. 1982. Multvariate Analysis in Community Ecology. Cambridge University Press, Cambridge.

Habeck, J. R. 1961. The original vegetation of the mid-Willamette Valley, Oregon. Northw. Sci. 35:65-77.

Heltsche, J. F., and N. E. Forrester. 1983. Estimating species richness using the jackknife procedure. Biometrics 39:1-11.

Hill, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. Ecol. 54:427-432.

_____. 1979a. TWINSPAN—a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Ecol. and Systematics, Cornell University, Ithaca, New York.

_____. 1979b. DECORANA—a FORTRAN program for detrended correspondence analysis and reciprocal averaging. Ecol. and Systematics, Cornell University, Ithaca, New York.

Hitchcock, C. L., and A. S. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle.

Johannessen, C. L., W. A. Davenport, A. Millet, and S. McWilliams. 1971. The vegetation of the Willamette Valley. Ann. Assoc. Amer. Geogr. 61:286-302.

Keniston, J. A. 1978. Program CLUSTER: an aid to numerical classification using the CDC CYBER computer. Unpublished report. Pleuronectid Proj. Tech. Rep. 2, Oregon State University Sea Grant Progr., Corvallis.

Knezevich, C. A. 1975. Soil Survey of Benton County Area, Oregon. USDA Soil Cons. Serv., Washington, D.C.

Lee, L. C., T. M. Hinckley, and M. L. Scott. 1985. Plant water status relationships among major floodplain sites of the Flathead River, Montana. Wetlands 5:15-34.

Maarel, E. van der, J. G. M. Janssen, and J. M. W. Louppen. 1978. TABORD, a program for structuring phytosociological tables. Vegetatio 83:143-156.

Marshall, J. L. 1985. Value assessment of Jackson-Frazier Wetland. Oregon State University, Corvallis. M.S. Thesis.

Moir, W., and P. Mika. 1972. Prairie vegetation of the Willamette Valley, Benton County, Oregon. Unpublished report on file at USDA For. Serv. Forestry Sci. Lab., Corvallis, Oregon.

Owston, P. W. In press. Oleaceae, olive family, *Fraxinus latifolia* Benth., Oregon ash. Editorial draft for Silvics Manual on file at the USDA For. Serv. Forestry Sci. Lab., Corvallis, Oregon.

Thilenius, J. F. 1968. The *Quercus garryana* forests of the Willamette Valley, Oregon. Ecol. 49:1124-1133.

Towle, J. C. 1982. Changing geography of Willamette Valley woodland. Oregon Hist. Quart. 83:66-87.

Sprague, F. L. and H. P. Hansen. 1946. Forest succession in the McDonald Forest, Willamette Valley, Oregon locality. Northw. Sci. 20:89-98.

Walter, H., and H. Lieth. 1967. Klimadiagramm-Weltatlas. VEB Gustav Fischer Verlag, Jena.

Received 21 November 1986
Accepted for publication 8 July 1987

William L. Gaines, and **Richard E. Fitzner,** Applied Ecology Section,
Pacific Northwest Laboratory, P.O. Box 999, Richland, Washington 99352

Winter Diet of the Harlequin Duck at Sequim Bay, Puget Sound, Washington

Abstract

Little information is available concerning the diet of harlequin ducks (*Histrionicus histrionicus*), therefore we examined their diet in Sequim Bay, Puget Sound, WA. We analyzed esophagi and gizzard contents of 21 harlequin ducks collected during the winter at the mouth of Sequim Bay. Principal food items were found to be snails, limpets, crabs, and chitons. Most of the prey of the harlequin duck was associated with rocky areas. Results of this study indicate that rocky shoreline areas are very important to harlequin ducks and should be protected.

Introduction

The distribution of harlequin ducks (*Histrionicus histrionicus*) includes the Pacific coastline from Alaska to central California (Bellrose 1976). Cottam (1939) discovered that crustaceans and molluscs made up most of the diet of harlequin ducks collected from Alaska, British Columbia, Quebec, Alberta and California. Vermeer (1983) provided a detailed dietary analysis of harlequin ducks from the Strait of Georgia, British Columbia, and he showed that their principal food items were snails, limpets, fish eggs, crabs, chitons, algae, and bivalves. Hirsch (1980) gave information on the foraging habitats, but not the diet, of harlequin ducks in Puget Sound, Washington. Our objective was to acquire information on the diet of wintering harlequin ducks at Sequim Bay, Puget Sound, Washington, as none of the earlier studies provide these data.

Methods

Harlequin ducks were collected at the mouth of Sequim Bay during November, December and January from 1982 through 1985. Contents of esophagi and gizzards were removed from 21 ducks (14 males and 7 females) and preserved in formalin. These contents were then sorted into taxa using a dissecting scope. Total volume, percent of volume and number of individuals were determined for each prey taxa. Kozloff (1974) identified the habitats of many invertebrates in Puget Sound and we used these data to make prey species habitat associations in order to establish the feeding habitat preferences of harlequin ducks.

Results and Discussion

The principal food items were snails, limpets, crabs, and chitons (Table 1). The snail, *Littorina scutulata,* was the most common species found in the ducks' diet (24.6%). Vermeer (1983) noticed many hermit crabs (*Pagurus* sp.) within *Littorina* shells and suggested they were consumed along with the shells. However, few *Littorina* shells contained hermit crabs in this investigation. *Notoacmaea* spp. was the most common limpet and second most abundant food item. *Hemigrapus oregonensis* and *Mopalia* spp. were respectively the most common crab and chiton consumed. Our results show the diet of harlequin ducks in Sequim Bay and the Strait of Georgia (Vermeer 1983) to be very similar. The only significant difference was the presence of fish eggs in the diet of ducks collected from the Strait of Georgia (Vermeer 1983). We found no fish eggs in the esophagi or gizzards examined, probably due to the time of year at which the birds were collected.

The habitat preferences of the prey items consumed suggest they were eaten while the ducks were feeding among rocks. For example, 67 percent of harlequin duck prey was associated with rocky areas, 13 percent with sandy areas, and 20 percent with seaweeds (kelp—*Alaria* spp. and *Macrocystis* spp., eelgrass—*Zostera marina*). Hirsch (1980) noted that harlequin ducks preferred shallow eelgrass and kelp communities close to shore. When making our collections, we observed that harlequin ducks fed near shore (within 50 m) over cobble to cobble/rock substrate of gradual gradient, and over sand substrate of gradual gradient containing eelgrass or kelp vegetation. Both our research and that of Vermeer (1983) showed these areas to be important feeding habitats of

TABLE 1. Winter foods of harlequin ducks from Sequim Bay, Washington, 1982 to 1985.

Food Type	Volume (ml)	Percent volume	No. indiv.
Snails			
Littorina scutulata	15.5	24.6	262
Lacuna spp.	1.1	1.7	22
Nucella emarginata	.8	1.3	4
Nassarius mendicus	.5	.8	4
Margarites pupillus	.1	.2	2
Unident. fragments	.5	.8	
(Total snails)	(18.5)	(29.4)	(294)
Limpets			
Notoacmaea spp.	11.9	18.9	101
Collisella pelta	1.4	2.2	11
Acmea mitra	.4	.6	1
Colisella instabilis	.2	.3	1
(Total limpets)	(13.9)	(22.0)	(114)
Crabs			
Hemigrapus oregonensis	7.1	11.4	4
Cancer spp.	.9	1.4	1
Pagurus spp.	.3	.5	5
Unident. fragments	1.4	2.2	
(Total crabs)	(9.7)	(15.5)	(10)
Chitons			
Mopalia spp.	6.6	10.5	144
Bivalves			
Mytilus edulis	.1	.2	1
Unident. fragments	.5	.8	
(Total bivalves)	(.6)	(1.0)	(1)
Shrimp			
Jassa falcata	.4	.6	2
unident. fragments	.7	1.1	
(Total shrimp)	(1.1)	(1.7)	(2)
Miscellaneous			
Idotea spp.	2.4	3.8	2
Unident. fragments	10.1	16.1	
TOTALS	62.9	100.0	567

harlequin ducks so rocky shores and seaweed areas should be identified in Puget Sound and protected from catastrophies such as oil spills and other pollutants.

Acknowledgements

This work was supported by the United States Department of Energy under Contract DE-AC06-76RLO 1830. We gratefully acknowledge the support of the Northwest College and University Association for Sciences (NORCUS) and the Pacific Northwest Laboratory.

Literature Cited

Bellrose, F. C. 1976. Ducks, geese, and swans of North America. Stackpole Books.

Cottam, C. 1939. Food habits of North American diving ducks. U.S. Dept. of Agric. Tech. Bull. 643.

Hirsch, K. V. 1980. Winter ecology of sea ducks in the inland marine waters of Washington. University of Washington, Seattle. M.S. Thesis.

Kozloff, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago and adjacent regions. Univ. Washington Press, Seattle.

Vermeer, K. 1983. Diet of the harlequin duck in the Strait of Georgia, British Columbia. The Murrelet 64:54-57.

Received 13 March 1987
Accepted for publication 2 July 1987

Steven J. Kozel and **Wayne A. Hubert,**
Wyoming Cooperative Fish and Wildlife Research Unit[1],
University of Wyoming, Laramie, Wyoming 82070

Age Estimates of Brook Trout from High-elevation Rocky Mountain Streams using Scales and Otoliths

Abstract

It is important to know the age structure of fish populations when setting management policies. However, techniques for aging fish have met with mixed results. To test reliability of two techniques, age estimates were made from scales and otoliths for brook trout, *Salvelinus fontinalis,* collected at elevations of 2750 m and 3200 m above mean sea level in the Snowy Range of the Rocky Mountains, southeastern Wyoming. Our results indicated that age estimates from otoliths tended to be higher than those from scales. Agreement was poor between independent estimates by different readers, and between separate estimates by a single reader, for both structures. Neither scales nor otoliths produced reliable age estimates for brook trout from high-elevation streams.

Introduction

The use of scales and otoliths to age brook trout have had mixed results. Scales have been shown to be a valid structure for aging brook trout, *Salvelinus fontinalis* (Cooper 1951, Konapachy 1978), but several investigators have reported difficulty in reading scales from fish in slow-growing populations (King 1942, Wilder 1952, Reimers 1958, Rabe and Dyer 1964). Furthermore, otoliths yielded higher age estimates than scales for stream-dwelling brook trout collected north of latitude 56°N (Grande 1964, Dutil and Power 1977). Konapacky (1978), however, found little difference between age determinations using otoliths and scales for brook trout from the Appalachian Mountains of Eastern United States.

To our knowledge, a comparison of otoliths and scales for aging brook trout from high-elevation (>2500 m above mean sea level) streams in the Rocky Mountains has not previously been made. The objectives of our study were to (1) determine whether age determinations based on otoliths and scales from brook trout in high-elevation streams were similar, (2) determine if aging precision by separate readers differed between otoliths and scales taken from brook trout in these streams, and (3) describe the extent of variation in age determinations by a single reader between independent readings of each structure for these fish.

Study Area and Methods

Brook trout were collected by electrofishing during summer 1985 from two streams in the Medicine Bow National Forest—Telephone Creek (elevation above mean sea level at the sampling site, 3200 m) and Coon Creek (2750 m). Both streams are in a subalpine zone with a six- to seven-month winter period of snow and ice cover, when water temperatures are about 1°C; they do not exceed 10°C through the ice-free period.

Scales were removed from a point above the lateral line near the dorsal fin. They were prepared in the laboratory by merely soaking them in water in a Petri dish for several minutes for cleaning. Scales were magnified (90X) and photocopied with a microfiche copier.

We removed otoliths through the roof of the mouth, following the procedure described by Schneidervin and Hubert (1986). Otoliths were soaked in anise oil for six weeks to clear and then read with a dissecting microscope. Otoliths were placed on a microscope slide with a drop of toluene to remove the anise oil residue. A light source was placed at an angle to the microscope stage, which had been covered with a black plastic sheet.

Annuli on both scales and otoliths were identified using the criteria of Lux (1971). Two independent readings of each structure by a single reader were conducted. Two additional readers made one independent reading of each structure. The first reading of the first reader and the readings of the two additional readers were used to estimate fish age for a particular structure.

[1]The Unit is jointly supported by the University of Wyoming, the Wyoming Game and Fish Department and the U.S. Fish and Wildlife Service.

When at least two readings were in agreement, that agreed upon age was used. When no agreement was achieved among the three readers, the median value was used.

Results

The data from all 165 brook trout collected from the two streams were pooled for analysis. Both scales and otoliths indicated slow growth. The average total lengths of brook trout in the sample at different ages, as estimated by the two methods, were as follows (n = sample size):

Age	*Scales*	*Otoliths*
I	120(9)	102(10)
II	127(52)	116(23)
III	174(66)	130(27)
IV	190(36)	189(51)
V	194(2)	—

No growth was detected using otoliths beyond age IV (n = 54) to the maximum estimated age of IX. A significant difference was observed when the frequency histogram of estimated ages based on scales was compared with that based on otoliths (chi-square = 93.5, df = 8, $P \leq 0.01$; Figure 1). When scales were used the modal age of fish collected was three years (range, 1-5 years); when otoliths were used the modal value was four years (range, 1-9 years).

Otoliths tended to yield higher age estimates than did scales for all ages (Figure 2); individual differences were as great as five years. Ages based on otoliths were higher than those based on scales in 64 percent of the fish studied; ages determined from the two structures agreed for 27 percent of the fish.

The independent readings of three trained readers differed significantly for both otoliths (chi-square = 37.7, df = 18, $P \leq 0.01$) and scales (chi-square = 80.3, df = 12, $P \leq 0.01$). The agreement between two separate age determinations by a single reader was only 48 percent for otoliths and 55 percent for scales.

Age determinations by a single reader differed by as much as four years when otoliths were used and three years when scales were used. A one-year age difference occurred in 44 percent of the fish when otoliths were used and in 39 percent when scales were used.

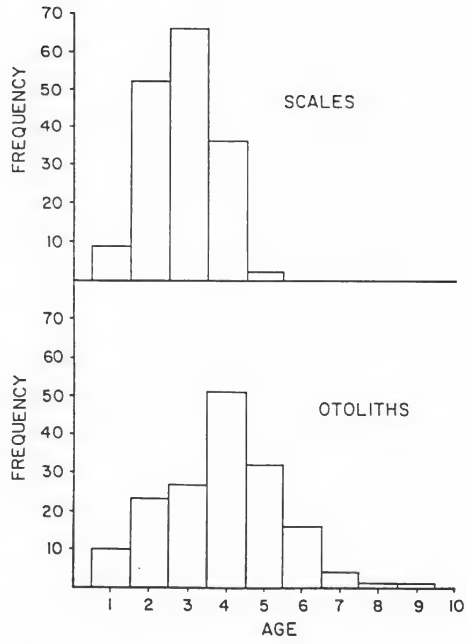

Figure 1. Frequency histograms for estimated ages based on scales and otoliths from brook trout.

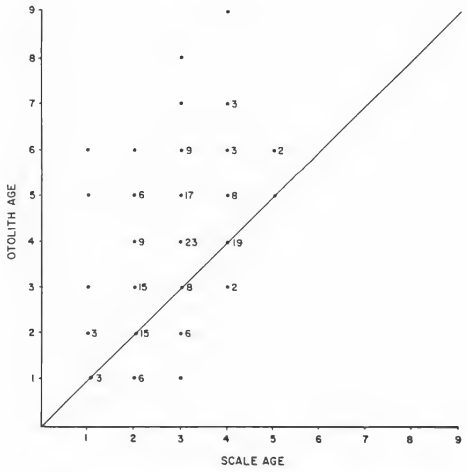

Figure 2. Comparison of age estimates for brook trout based on otoliths and scales. Points represent individual fish except where indicated by numbers. Points on the diagonal line indicate equal age estimates for both structures.

Discussion

Otoliths tended to indicate older ages than scales in this sample of brook trout from high-elevation Rocky Mountain streams. Similar results were observed at more northern latitudes by Grande, 1964; and Dutil and Power, 1977. Grande (1964) observed good correlations between scales and otoliths for the first three years, but differed thereafter with maximum age of scale-aged fish being six years and of otolith-aged fish being eight years. Dutil and Power (1977) observed consistent differences with the maximum age of scale-aged fish being eight years and otolith-age fish being ten years. Such differences, however, were not observed for stream dwelling brook trout at moderate elevations in lower latitudes of the Appalachian Mountains (Konopacky 1978).

Otoliths and scales have been used to estimate the age of other slow-growing fishes in north temperate latitudes, e.g., Arctic grayling, *Thymallus arcticus* (Sikstrom 1983); lake whitefish, *Coregonos clupeaformis* (Barnes and Power 1984); round whitefish, *Prosopuim cylindraceum* (Jessop 1972); cisco or lake herring, *Coregonus artedii* (Morin 1980); longnose sucker, *Catostomus catostomus* (Tripp and McCart 1974); and cutthroat trout, *Salmo clarki* (Hubert *et al.* 1987). In general, few differences between ages determined from scales and from otoliths were observed among young fish, but estimates based on otoliths were consistently older than those based on scales for older fish. Evaluation of aging precision has generally not been made; the only known assessment with a salmonid was by Hubert *et al.* (1987) for cutthroat trout from Yellowstone Lake where poor precision was also observed.

Neither scales nor otoliths appeared to yield sound estimates of age in our sample of brook trout from high-elevation streams. Substantial variation in age determination was observed among independent readers and between readings by one reader with either structure. The inconsistent growth pattern expressed by the average total lengths at annulus formation in our sample is believed to be due to the imprecision of aging among readers and the statistics should not be considered as accurate estimates of growth for either otolith-aged or scale-aged fish. Use of either otoliths or scales is imprecise. Summary statistics developed from such data must be considered merely as rough estimates. Such a conclusion is important to management agencies that use such information to establish regulations and control exploitation.

Validation of otoliths as an aging technique suitable for slow-growing brook trout from high-elevation mountain streams is needed. Although differences were observed between otoliths and scales, we did not determine which structure provided the more accurate estimate of age.

Acknowledgements

We thank J. Hart for field assistance; and J. Lessard and M. Tiezen for laboratory assistance. This study was supported by the Wyoming Cooperative Fish and Wildlife Research Unit.

Literature Cited

Barnes, M. A., and G. Power. 1984. A comparison of otolith and scale ages for western Labrador lake whitefish, *Coregonus clupeaformis*. Environ. Biol. Fish 10:297-299.

Cooper, E. L. 1951. Validation of the use of scales of brook trout, *Salvelinus fontinalis,* for age determination. Copeia 1951:141-148.

Dutil, J. D., and G. Power. 1977. Validity of reading otoliths compared to reading scales for determination of age of brook trout (*Salvelinus fontinalis*). Nat. Can. 104:361-367.

Grande, M. 1964. Age determinations from scales and otoliths in the brook trout (*Salvelinus fontinalis*). Nytt Mag. Zoology 12:35-37.

Hubert, W. A., G. T. Baxter, and M. Harrington. 1987. Comparison of age determinations based on scales, otoliths and fin rays for cutthroat trout from Yellowstone Lake. Northw. Sci. 61:32-36.

Jessop, B. M. 1972. Aging round whitefish (*Prosopium cylindraceum*) of the Leaf River, Ungava, Quebec, by otoliths. J. Fish. Res. Board Can. 452-454.

King, W. 1942. Trout management studies of Great Smoky Mountains National Park. J. Wildl. Manage. 6:147-161.

Konapacky, R. C. 1978. Age and growth analyses of thirty-two established populations of brook trout *Salvelinus fontinalis* (Mitchell). Tennessee Technological University, Cookville, Tennessee. M.S. Thesis.

Lux, F. E. 1971. Age determinations of fishes (Revised). U.S. National Marine Fisheries Service, Fisheries Leaflet 637. Pp. 1-7.

Morin, R. 1980. Ecology of anadromous coregonine fishes in estuaries of eastern James-Hudson Bay. Laval University, Quebec. M.S. Thesis.

Rabe, F. W., and V. E. Dyer. 1964. Age and growth study of brook trout from three cirque lakes in the Unita Mountains. Proc. Utah Acad. Sci. 41:243-254.

Reimers, N. 1958. Conditions of existence, growth and longevity of brook trout in a small, high altitude lake of the eastern Sierra Nevada. Calif. Fish Game 44:319-333.

Schneidervin, R. W., and W. A. Hubert. 1986. A rapid technique for otolith removal from salmonids and catostomids. No. Amer. J. Fish. Manage. 6:287.

Sikstrom, C. B. 1983. Otolith, pectoral fin ray, and scale age determinations for Arctic grayling. Prog. Fish-Cult. 45:220-223.

Tripp, D. B., and P. J. McCart. 1974. Life histories of grayling (*Thymallus arcticus*) and longnose suckers (*Catostomus catostomus*) in the Donelly River system, Northwest Territories. In Canadian Arctic Gas Study Limited. Biological Report Series. Vol. 20, Chap. 1.

Wilder, B. G. 1952. A comparative study of anadromous and fresh-water populations of brook trout (*Salvelinus fontinalis* Mitchell). J. Fish. Res. Board Can. 9:169-203.

Received 11 December 1986
Accepted for publication 1 July 1987

D. B. Houston, B. B. Moorhead, and **R. W. Olson,**
Olympic National Park, 600 E. Park Avenue, Port Angeles, Washington 98362

Roosevelt Elk Density in Old-Growth Forests of Olympic National Park

Abstract

We explored the feasibility of censusing Roosevelt elk from a helicopter in the dense old-growth forests of Olympic National Park, WA. Mean observed densities ranged from 8.0-11.6 elk/km^2, with coefficients of variation averaging 19.9 percent. A provisional sightability factor of 74 percent suggested that actual mean densities ranged from 10.8-16.0 elk/km^2. We conclude that estimates of elk density probably could be refined, but not without a cost and level of disturbance in the park that seem unwarranted at present. The effort required to conduct the 18 counts made during 1985-86 was substantial. For almost every successful count an unsuccessful attempt was made. These included aborting five flights when counting conditions turned sour. Actual counting time for the successful flights was 15.7 and 16.2 hours in 1985 and 1986, respectively. Additional flight time for traveling to and from the census zones, refueling, and aborted attempts added 12.2 and 10.8 hours for the respective years.

Introduction

The Roosevelt elk (*Cervus elaphus roosevelti*) of Olympic National Park represent the last large populations of this subspecies that are relatively undisturbed in their natural habitat. Recent studies have added considerably to knowledge of elk-habitat relationships, social organization, and nutrition (Jenkins and Starkey 1982, 1984; Leslie *et al.* 1984). Techniques have not been developed to determine densities and population trends, primarily because elk occupy dense, old-growth coniferous forests. Moreover, there seemed to be no pressing need to do so; studies indicated that populations occurred at ecological carrying capacity with stable elk-vegetation relationships (C. Newman pers. comm.; Jenkins 1979, 1981; Leslie *et al.* 1984).

This laissez-faire management changed dramatically in 1984. A preliminary legal opinion (Weinberg 1984) indicated that Indian tribes retained hunting privileges within Olympic National Park stemming from the Treaty of Olympia, signed in 1856. Park managers directed that studies be undertaken to develop techniques to measure elk densities since the possibility now arose that these populations would be harvested.

Little empirical information has been published on either the density of Roosevelt elk or techniques suitable to measure density. Reported densities often are educated guesses or are calculated from estimates of herd composition and harvest for exploited populations (R. D. Taber pers. comm.). The usual indices of relative abundance appear to be of limited practical value in the Olympics: e.g., pellet group surveys present formidable sampling problems because the pellets decompose so rapidly (Fairbanks 1978).

The Olympic elk were known to undergo a major shift in habitat use with spring growth of herbaceous vegetation (Jenkins and Starkey 1982)—this apparently occurring just before leafout and subsequent canopy closure of deciduous trees. We took advantage of these earlier findings to explore the seemingly remote feasibility of aerial census. Preliminary helicopter counts conducted in 1984 suggested that substantial numbers of elk could indeed be observed during this brief, 2-3 week, period (Houston, unpublished). We report here the results from aerial census of Roosevelt elk carried out between 1984 and 1986. The primary objectives were: (1) to evaluate the precision (stability) of the index counts, and (2) to calibrate the counts to improve accuracy by using observations of radio-collared elk (Floyd *et al.* 1979, Samuel 1984).

Study Area and Methods

The census zones established on the Hoh, South Fork (SF) Hoh, and Queets River drainages covered the valley floors, and were bounded laterally by the steep valley walls (Figure 1). Two small census units established in 1984 (Areas "A") for preliminary surveys were expanded as shown. The U-shaped valleys are 1-3 km wide, and contain at least four river terraces of successively greater age (Fonda 1974, McKee *et al.* 1982, Tabor and Cady 1978). Elevations range

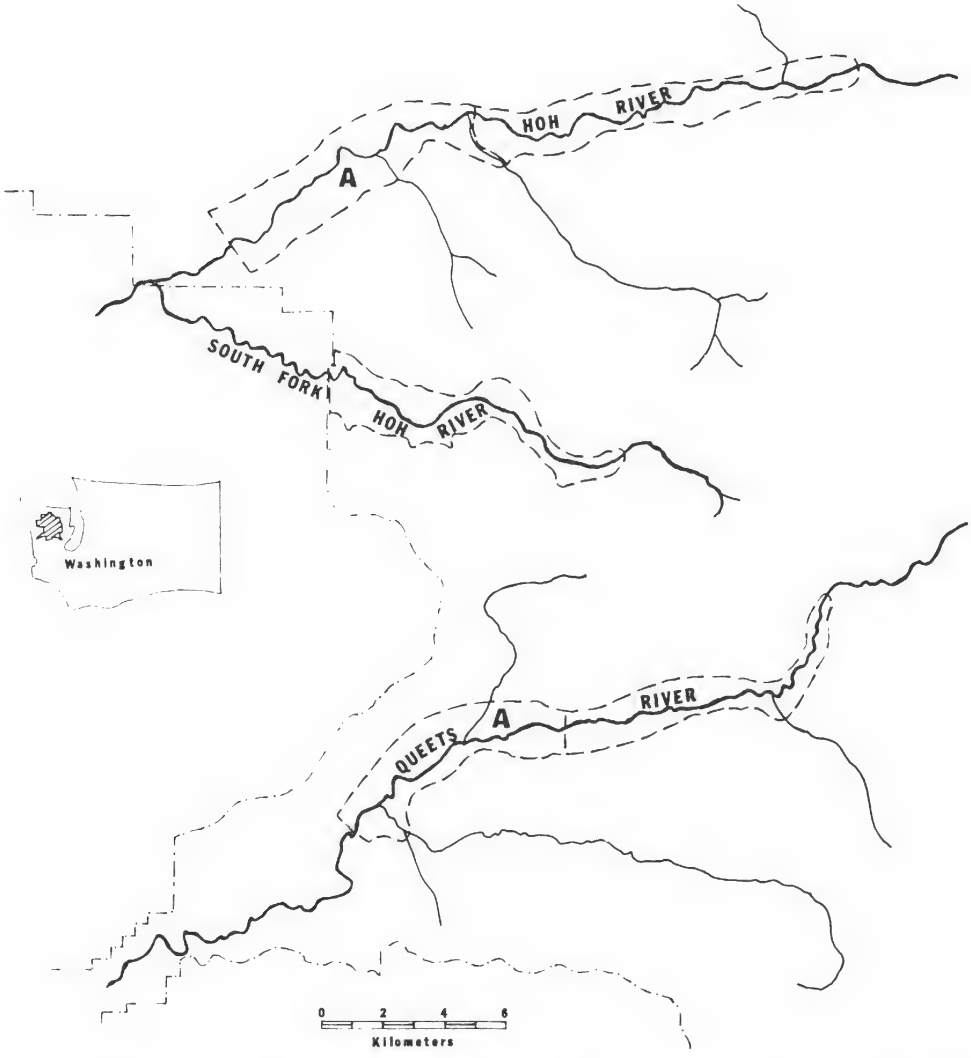

Figure 1. Elk census zones, Olympic National Park, 1985 and 1986. Areas "A" on mainstem Hoh and Queets Rivers were also censused during 1984. Queets Unit A = 11.0 km²; Total 19.4 km². Hoh Unit A = 11.5 km²; Total 23.4 km². S.F. Hoh = 11.1 km².

from 135 to 335 m. Precipitation ranges from 300 to 460 cm, with about 75 percent falling (mostly as rain) from November-April.

Forests of the census zones have been described as a sere from pioneer red alder (*Alnus rubra*) on active floodplains, through black cottonwood (*Populus trichocarpa*)-Sitka spruce (*Picea sitchensis*) on the younger terraces, to stands of western hemlock (*Tsuga heterophylla*) and Sitka spruce on older terraces. Groves of big leaf maple (*Acer macrophyllum*) occur throughout on shallow rocky soils. The coniferous forests are characterized by massive trees up to 90 m tall at densities of about 60-270 trees/ha (Fonda 1974, McKee *et al.* 1982).

The distribution and composition of the herbaceous understory vegetation within the forest communities on the census zones are particularly relevant to elk diets and sightability. Grasses and forbs dominate the herb layer on floodplains and the first river terraces. Grasses are largely absent from the older terraces; mosses and ferns predominate (Fonda 1974, McKee *et al.* 1982). The combined biomass of grasses and forbs is much greater in stands of deciduous trees and in forest clearings than in the mature conifer forest on the older terraces (Leslie 1983:77).

Forests of the adjacent valley walls are similar to those of the montane zone. Stands are dominated by massive red cedar (*Thuja plicata*), Douglas-fir (*Pseudotsuga menziesii*), silver fir (*Abies amabilis*), and western hemlock. Densities are greater than on the valley bottom census zones, ranging from 400-600 trees/ha. The herb layer is sparse (Fonda and Bliss 1969, Fonda 1974). Wall forests are layered and canopy cover is virtually complete. Consequently, the forest floor was essentially invisible during helicopter census, and the walls were excluded from the census zones.

Elk show two different life history patterns in the census zones: (1) year-round residence, and (2) seasonal migrations to high elevation summer ranges (Schwartz and Mitchell 1945, C. Newman, personal comm., Jenkins 1979, Jenkins and Starkey 1982, Houston, Moorhead and Olson unpubl.). Resident cow-calf groups on the Hoh show high group constancy and have home ranges averaging about 11 km^2. Elk use shifts primarily to the valley floor during March. Red alder and cottonwood-spruce forests receive peak use in late winter as greenup begins, and grasses and forbs become increasingly important in elk diets (Jenkins and Starkey 1982, 1984, Leslie *et al.* 1984). This documented shift in elk distribution to more open forest types on the valley floor is crucial to the census.

Observations suggest that resident and migratory elk showed similar patterns of habitat use during the census periods. High elevation areas were still snow-covered and unavailable to migrants. Also, a radio-collared female elk, known to migrate to summer ranges, was always present during the counts.

Preliminary counts in 1984 suggested that the censuses should be conducted early in the morning, on overcast days, and with search intensities of at least 4 min/km^2 (Houston, unpublished). Census design consisted of repetitive surveys of the zones at treetop level ($\sim$100 m) using a Hughes 500D helicopter. A pilot, a navigator-observer, and two observers made up the census team. The search pattern consisted of slow (25-30 knot) zigzag coverage across the axis of the river. Conditions recorded during each flight included: cloudcover, snowcover, temperature, windspeed, extent of greenup of the herb layer, and phenology of hardwoods. The location of each elk group was plotted on 1:62,500 scale maps and, for 1985 and 1986, on 1:12,000 aerial photos.

Elk were immobilized with capture darts containing either M_{99} or carfentanil (Hebert *et al.* 1982, Meuleman *et al.* 1984) and fitted with radio collars (Telonics Model 5 or 6B). The census was conducted with the telemetry scanner-receiver (Telonics Model TR2-TS1) turned off. When a collared elk was observed, the receiver was turned on for a few seconds to identify the animal and then switched off. The remaining, unobserved, collared elk were located by telemetry after the census.

The observability of radio-collared elk was used to develop correction factors to improve census accuracy, following Floyd *et al.* (1979) and Samuel (1984). A sightability factor developed for elk *groups* on the Queets census area was applied to all zones. Corrected elk densities were calculated by estimating the number of groups actually present and then multiplying these values by the mean group size observed in each zone.

Results and Discussion

Counts were variable, but numbers did not differ significantly (Wilcoxon Two Sample tests $P > 0.10$) between 1985 and 1986 for any zone (Table 1). The 1984 counts were obtained under conditions generally comparable to 1985 and 1986, but counting time was less than in later years (4.48 ± 0.50 vs. 5.99 ± 0.62 min/km^2) and there were minor differences in the lateral boundaries of Units A. Although the 1984 counts also do not differ from more recent counts, the 1985-86 counts represent our best efforts as the census team gained experience. Coefficients of variation (CV) averaged 19.9 percent over the three zones during 1985-86. Precision of the counts on the larger zones of the Hoh and Queets was greater (CV's $\sim$15%) than on smaller units ($\sim$30-33% for SF Hoh and Units "A"). Improved precision on the larger units may have resulted from including the entire valley bottom home ranges of more elk. Several times

TABLE 1. Elk counted on the Hoh and Queets Rivers, 1984-1986.

Area	Date	Elk Numbers		Elk/km²	
		Unit A	Total	Unit A	Total
Queets	1984				
	3/13	83		7.6	
	3/19	189		17.2	
	3/27	122		11.1	
	$\bar{x} \pm SE$[1]	131.3 ± 30.95		12.0 ± 2.80	
	1985				
	3/20	95	261	8.6	13.5
	3/29	58	163	5.3	8.4
	4/13	170	250	15.5	12.9
	$\bar{x} \pm SE$	107.6 ± 32.95	224.6 ± 31.00	9.8 ± 3.00	11.6 ± 1.61
	1986				
	3/22	128	262	11.6	13.5
	3/29	121	215	11.0	11.1
	4/3	104	224	9.5	11.5
	$\bar{x} \pm SE$	117.6 ± 7.13	233.6 ± 14.40	10.7 ± 0.62	12.0 ± 0.74
	Overall $\bar{x} \pm SE$	118.8 ± 13.64	229.2 ± 15.42	10.8 ± 1.24	11.8 ± 0.80
	CV[2]	33.4	15.6		
Hoh	1984				
	3/13	121		10.5	
	3/19	103		9.0	
	3/27	121		10.5	
	$\bar{x} \pm SE$	115.0 ± 6.00		10.0 ± 0.50	
	1985				
	3/19	103	174	9.0	7.4
	3/25	49	144	4.3	6.2[3]
	4/4	55	186	4.8	8.0
	$\bar{x} \pm SE$	69.0 ± 17.08	168.0 ± 12.49	6.0 ± 1.49	7.2 ± 0.53
	1986				
	3/17	85	211	7.4	9.0
	3/25	60	222	5.2	9.5
	4/2	62	185	5.4	7.9
	$\bar{x} \pm SE$	69.0 ± 8.02	206.0 ± 10.97	6.0 ± 0.70	8.8 ± 0.47
	Overall $\bar{x} \pm SE$	84.3 ± 9.56	187.0 ± 11.29	7.3 ± 0.83	8.0 ± 0.48
	CV	33.0	14.0		
SF Hoh	1985				
	3/21		90		8.1[3]
	4/1		123		11.1
	4/12		130		11.7
	$\bar{x} \pm SE$		114.3 ± 12.33		10.3 ± 1.11
	1986				
	3/20		104		9.4
	3/23		45		4.1
	3/31		87		7.8
	$\bar{x} \pm SE$	78.6 ± 17.53	7.1 ± 1.57		
	Overall $\bar{x} \pm SE$		96.5 ± 17.64		8.7 ± 1.12
	CV		30.1		

1. Mean ± standard error.
2. Coefficient of variation as %, corrected for sample size (Sokal and Rohlf 1981:59). CV for elk/km² similar to those for elk numbers.
3. 3-20 cm new snow on Hoh prior to count; 3-5 cm on SF Hoh.

during 1984 (and SF Hoh in 1986) one or more groups of elk were observed alternately inside and then just outside established census units, indicating that boundaries bisected home ranges.

Two low counts on the SF and mainstem Hoh occurred immediately after snowstorms (Table 1), suggesting that elk moved off the zones. This was also indicated by the locations of elk that were observed; many occurred at the bases of valley walls. Elk are known to leave floodplains and move onto valley walls during winter snows (Jenkins and Starkey 1984). We could find no environmental explanation for several other low counts, so including the snowfall counts in calculations made little difference to precision.

Mean observed elk densities ranged from 8.0-11.6/km² for 1985-86 and were highest (Wilcoxon Two sample, $P < .05$) on the Queets. Maximum observed densities ranged from 9.5-13.5/km². Mean observed group size ranged from 11.6-13.3 elk and did not differ among years or areas (Table 2). Mean group size was smaller than the spring mean of 27 reported earlier from the Hoh (Jenkins and Starkey 1982) because our sample included small groups of bull elk in addition to the cow-calf groups.

TABLE 2. Observed elk group size, 1984-86.

Area	Years	Group Size	
		N	X ± Std Dev (Range)
Queets	1984-86	133	13.3 ± 11.9 (1-61)
Hoh	1984-86	123	11.9 ± 10.0 (1-43)
S.F. Hoh	1985-86	50	11.6 ± 14 (1-46)

A provisional sightability factor of 74 percent was derived from 19 encounters with groups containing radio-collared elk (14 groups observed, 5 missed). [High mortality damaged efforts to determine sightability. Seven elk fitted with transmitters in the Queets census zone in 1985 had been reduced to two by the middle of the 1986 census period, mainly by cougar (*Felis concolor*) predation.] The provisional adjustment returned actual mean densities of about 16.0, 10.8 and 11.7 elk/km² on the Queets, Hoh and SF Hoh, respectively. We recognize that group size influences elk sightability (Samuel 1984), but size did not differ between sighted ($X = 23.7 \pm 10.79$ elk) and unsighted groups (13.6 ± 14.17, $P > .05$, Wilcoxon Two sample) for these few observations.

The precision of the index counts encountered during the elk census (CV's 15-33%) is apparently in the range expected for many wild populations (Le Resche and Rausch 1974, Eberhardt 1978, Beasom 1979, Beasom *et al.* 1986, Harris 1986), particularly under difficult survey conditions. Approximate 95 percent confidence limits (Sokal and Rohlf 1981:148) for the mean counts of 1985-86 were 229 ± 40, 187 ± 29 and 96 ± 45 elk for the Queets, Hoh, and SF Hoh, respectively. These limits may give a preliminary indication of the amount of change necessary to detect real population trends.

Interpretation of the counts requires caution because the entire home ranges of the elk could not be included in the zones. Even though elk use was concentrated on the valley floors, part of the variation among counts surely resulted from elk moving to the valley walls where they could not be observed. However, earlier studies of habitat use and diet, plus 45 March-April radio locations of 10 collared elk during the present study (including 5 elk downstream from the zone) suggest that a very high proportion of the combined resident and seasonally migratory populations occupy the valley floor during the census period. Circumstances of the census did not permit complete sex and age composition tallies, but adult males appeared to be well represented in the counts.

Despite the recognized limitations of the counts, the observed elk densities are instructive, and apparently represent the only empirical data on Roosevelt elk densities. These estimates begin to provide a quantitative perspective for Raedeke and Taber's (1982) speculation that high Roosevelt elk densities occurred historically along floodplains.

Acknowledgements

We thank Graeme Caughley, Lee Eberhardt, Kurt Jenkins, Ed Starkey and Mike Samuel for suggestions on study design. Jim Mott of Eagle Air Helicopters piloted the censuses. Rangers Hunter Sharp, Clay Butler and Allen King served as observers on several flights. The ranger staff of Olympic Park, especially Clay Butler, contributed substantially to the efforts to capture elk. K. Jenkins, E. Schreiner, E. Starkey, M. Samuel, J. Matthews, J. Burger and L. Eberhardt reviewed the manuscript. V. Rose typed the manuscript.

Literature Cited

Beasom, S. L. 1979. Precision in helicopter censusing of white-tailed deer. J. Wildl. Manage. 43:777-779.

Beasom, S. L., F. G. Leon, and D. R. Synatzske. 1986. Accuracy and precision of counting white-tailed deer with helicopters at different sampling intensities. Wildl. Soc. Bull. 14:364-368.

Eberhardt, L. L. 1978. Appraising variability in population studies. J. Wildl. Manage. 42:207-238.

Fairbanks, R. L. 1978. An evaluation of the pellet-group survey as a deer and elk census method in western Washington. University of Washington, Seattle. M.S. Thesis.

Floyd, T. J., L. D. Mech, and M. E. Nelson. 1979. An improved method of censusing deer in deciduous-coniferous forests. J. Wildl. Manage. 43:258-261.

Fonda, R. W. 1974. Forest succession in relation to river terrace development in Olympic National Park, Wa. Ecology 55:927-942.

Fonda, R. W., and L. C. Bliss. 1969. Forest vegetation of the Montane and Subalpine Zones, Olympic Mountains, Wa. Ecol. Mono. 39:271-301.

Harris, R. B. 1986. Reliability of trend lines obtained from variable counts. J. Wildl. Manage. 50:165-171.

Hebert, D., D. Janz, K. Brunt, and J. Youds. 1982. Chemical immobilization of North American elk. *In* L. Nielsen, J. Haigh, M. Fowler (eds.). Chemical immobilization of N. Amer. Wildlife. Wisconsin Humane Soc. Milwaukee. Pp. 380-392.

Jenkins, K. J. 1979. Home ranges and habitat use by Roosevelt elk in Olympic National Park, Wa. Oregon State University, Corvallis. M.S. Thesis.

_____. 1981. Status of elk populations and lowland habitats in western Olympic National Park. Oregon Coop Park Studies Unit. Oregon State University, Corvallis. Report 81-1. 53 pp.

Jenkins, K. J., and E. E. Starkey. 1982. Social organization of Roosevelt elk in an old-growth forest. J. Mammal. 63:331-334.

_____. 1984. Habitat use by Roosevelt elk in unmanaged forests of the Hoh Valley, Washington. J. Wildl. Manage. 48:642-646.

Le Resche, R. E., and R. A. Rausch. 1974. Accuracy and precision of aerial moose censusing. J. Wildl. Manage. 38:175-182.

Leslie, D. M. 1983. Nutritional ecology of cervids in old-growth forests in Olympic National Park, Wa. Oregon State University, Corvallis. Ph.D. Dissertation.

Leslie, D. M., E. E. Starkey, and M. Vavra. 1984. Elk and deer diets in old-growth forests in western Washington. J. Wildl. Manage. 48:762-775.

McKee, A., G. La Roi, and J. F. Franklin. 1982. Structure, composition, and reproductive behavior of terrace forests, South Fork Hoh River, Olympic National Park. *In* E. E. Starkey, J. F. Franklin and J. W. Matthews (eds.). Ecological Research in Natl. Parks of the Pacific NW. Forest Research Lab Publn. Oregon State University, Corvallis. Pp. 22-29.

Meuleman, T., J. Port, T. Stanley, K. Willard, and J. Kimball. 1984. Immobilization of elk and moose with carfentanil. J. Wildl. Manage. 48:258-262.

Raedeke, K. J. and R. D. Taber. 1982. Mechanisms of population regulation in Western Washington forests for *Cervus* and *Odocoileus*. Trans. Intern. Congr. Game Biol. 14:69-79.

Samuel, D. M. 1984. An evaluation of elk sightability in North Central Idaho with application to aerial census and herd composition counts. University of Idaho, Moscow. Ph.D. Dissertation.

Schwartz, J. E., and G. E. Mitchell. 1945. The Roosevelt elk on the Olympic Peninsula, Wa. J. Wildl. Manage. 9:295-319.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman & Co. San Francisco.

Tabor, R. W., and W. M. Cady. 1978. Geologic map of the Olympic Peninsula, Wa. Misc. Investigations Series. U.S. Geol. Survey Publn.

Weinberg, J. L. 1984. Report and recommendation on motion to dismiss. Case No. CR82-332M. U.S. District Court, Western District of Washington at Seattle. 10 pp.

Received 19 March 1987
Accepted for publication 1 July 1987

Paul C. Fielder, Public Utility District No. 1 of Chelan County
P.O. Box 1231, Wenatchee, Washington 98801

and

Ronald G. Starkey[1], U.S. Fish and Wildlife Service, Ecological Services,
2625 Parkmont Lane, Olympia, Washington 98504

Bald Eagle Winter Abundance and Distribution in Eastern Washington

Abstract

We report monthly (November-March) wintering bald eagle (*Haliaeetus leucocephalus*) abundance and distribution, as determined from aerial surveys, along 11 major water bodies in eastern Washington for the winters of 1974-75 through 1983-84. Peak winter counts ranged from 98-209 eagles ($\bar{x} = 141.1$) along Banks Lake and the Columbia River between Pasco and Kettle Falls. Peak winter counts along the Spokane and Pend Oreille rivers ranged from 17-61 eagles ($\bar{x} = 31.6$). During the 10 winters surveyed, peak winter counts occurred in February seven times and January three times. Eagle numbers increased two-fold during the study period. Eagle densities were significantly greater along FDR Reservoir and Banks Lake and significantly less along the Columbia River from Rocky Reach Reservoir through the Hanford Reach, based upon shoreline availability and utilization analysis. Adult eagles were significantly more abundant along FDR and Chief Joseph reservoirs and significantly fewer along Wells Reservoir and the Hanford Reach.

Introduction

Washington has had the highest proportion (9-13%) of wintering bald eagles (*Haliaeetus leucocephalus*) in the lower 48 states since the National Wildlife Federation (NWF) mid-winter bald eagle survey began in 1979. Of the bald eagles reported in Washington during NWF surveys of 1979-1985 ($\bar{x} = 1466$, range = 1126-1876), 23 percent were reported in eastern Washington (east of the Cascade Mountain Range) (Wa. Dep. Game mid-winter bald eagle survey reports, 1979-1985).

Most bald eagles in the Pacific Northwest concentrate at salmon (*Oncorhynchus* spp.) spawning areas (Stalmaster *et al.* 1979, McClelland *et al.* 1982). However, eagles wintering in eastern Washington feed primarily on waterfowl, upland birds, big game and livestock carrion, and, to a lesser extent, fish (Fielder and Starkey 1980, Fitzner *et al.* 1980, Wood 1980, Fielder 1982). As a result, rather than being concentrated at salmon spawning areas, they are dispersed widely throughout eastern Washington.

Resource managers in eastern Washington are concerned with wintering bald eagles because: 1) bald eagles are protected under the Federal Endangered Species Act (U.S. Dep. Interior 1978), 2) more than 200 bald eagles annually winter along eastern Washington waters (Wa. Dep. Game mid-winter bald eagle survey reports, 1979-85), 3) wintering eagles often concentrate along rivers with hydroelectric dams because of the availability of food (Ingram 1965, Spencer 1976, Steenhof *et al.* 1980), and 4) because several hydroelectric modifications in eastern Washington have either recently occurred (e.g., raising elevations of Rock Island, Wells, and Chief Joseph reservoirs) or are anticipated. We present information on bald eagle abundance and distribution during the winters (November-March) of 1974-75 through 1983-84 along wintering areas in eastern Washington. Although NWF mid-winter surveys provide some information on eagle abundance and distribution, those surveys occur only during the first two weeks of January. Because of the transient habits of many wintering bald eagles (Young 1983), all areas used need identification, even if they are used for only a short period.

Study Area and Methods

Our survey area (Figure 1) included the Columbia River (from Pasco to about 10 km north of Kettle Falls), Banks Lake, the Spokane River (from its mouth to Spokane), and the Pend Oreille River (from Newport to Ione) and consisted of a total of 1775 km of shoreline. The Columbia River was surveyed according to the reservoirs behind the hydroelectric dams (Priest Rapids,

[1]Present address: 1811 8th Street N.E., East Wenatchee, WA 98801.

Wanapum, Rock Island, Rocky Reach, Wells, and Chief Joseph). The Hanford Reach included the Columbia River betwen Pasco and Priest Rapids Dam. Franklin D. Roosevelt (FDR) Reservoir lies behind Grand Coulee Dam and, for our purposes, extends from that dam to the upstream end of a large bay about 10 km north of Kettle Falls. The Spokane and Pend Oreille rivers were each treated as separate segments.

We conducted bald eagle surveys monthly (November-March) during the winters of 1974-75 through 1983-84, beginning in January 1975. The Spokane and Pend Oreille rivers were not surveyed during the winters of 1981-82 and 1982-83. The Columbia River (Pasco to 10 km north of Kettle Falls) and Banks Lake, were not surveyed during November 1981 or March 1983.

Surveys were conducted in a high-wing Cessna aircraft, flown at speeds of 130-145 km/h, 30-60 m above ground level, by an observer/pilot and one to three additional observers. Monthly surveys were flown within five days of the fifteenth of each month, conditionally upon weather allowing a minimum visibility of 3.2 km. Where river or reservoir width exceeded 0.8 km, each shoreline was flown separately. Where water body widths were 0.8 km or less, the route was flown along the center of the river, allowing both shores to be observed simultaneously. Eagles were classified as either adults or subadults; eagles with completely white heads and tails were classified as adults.

We attempted a complete count of the eagle population along our entire survey area during each survey. Although it is unlikely that all eagles within the survey area were seen during each survey, we assumed that the proportion of eagles seen was consistent during our surveys.

Trends in eagle abundance were identified by regression analysis and deviation of peak counts for each winter from 95 percent confidence intervals of the mean of the peak winter counts. Chi-squared and Bonferroni Z statistics (Neu *et al.* 1974) were used to analyze distribution and preference and avoidance of the Columbia River and Banks Lake water bodies. Differences in eagle age ratios along Banks Lake and Columbia River water bodies were analyzed by chi-squared analysis.

Results

Regression analysis ($r^2 = 0.76$) indicated an increasing trend within our Columbia River-Banks Lake study area of 10.2 eagles/winter between 1975 and 1984 (Figure 2, Table 1). Peak eagle counts for the winters of 1974-75, 1975-76, and 1976-77 were significantly less ($P < 0.05$) than the mean of the peak counts ($\bar{x} = 141.1$) and the peak counts for the winters of 1980-81 and 1981-82 were significantly ($P < 0.05$) greater within our survey area. During the winters of 1974-75 - 1979-80, eagle numbers along the mainstem Columbia River-Banks Lake survey area averaged 73, 98, and 109 eagles for December, January, and February, respectively (Table 1). This same area averaged 169, 162, and 158 eagles during those same respective months during the winters of 1980-81 - 1983-84. The winters of 1980-81 and 1981-82 were the winters of peak eagle abundance during January and February along the mainstem Columbia-Banks Lake survey area. The winter of 1983-84 had the highest November and March counts.

The overall increase in eagle numbers was influenced by increased numbers along FDR Reservoir and Banks Lake. Aerial surveys along these two water bodies during December 1975-79 averaged 22.6 eagles/survey compared to December 1980-84 surveys which averaged 119.3 eagles/survey. The remaining water bodies in our survey area (Hanford Reach-Chief Joseph Reservoir) showed no major changes in eagle numbers during our study.

Along the Spokane and Pend Oreille rivers, only peak counts for the winters of 1974-75 and 1979-80 varied significantly ($P < 0.05$) from the mean of the peak counts ($\bar{x} = 31.6$) during our survey period (Figure 2, Table 2).

Bald eagles were proportionally more abundant ($P < 0.05$) along FDR Reservoir and Banks Lake (Table 3). Banks Lake and FDR Reservoir comprised 32 percent of the shoreline of our mainstem Columbia River-Banks Lake survey area, but accounted for 50 percent, 57 percent, 45 percent, 41 percent, and 54 percent of the eagle sightings during the months of November-March, respectively. Availability and utilization data indicated that eagles used the portion of the Columbia River from Rocky Reach Reservoir through the Hanford Reach less ($P < 0.05$) than expected. This portion of our survey area

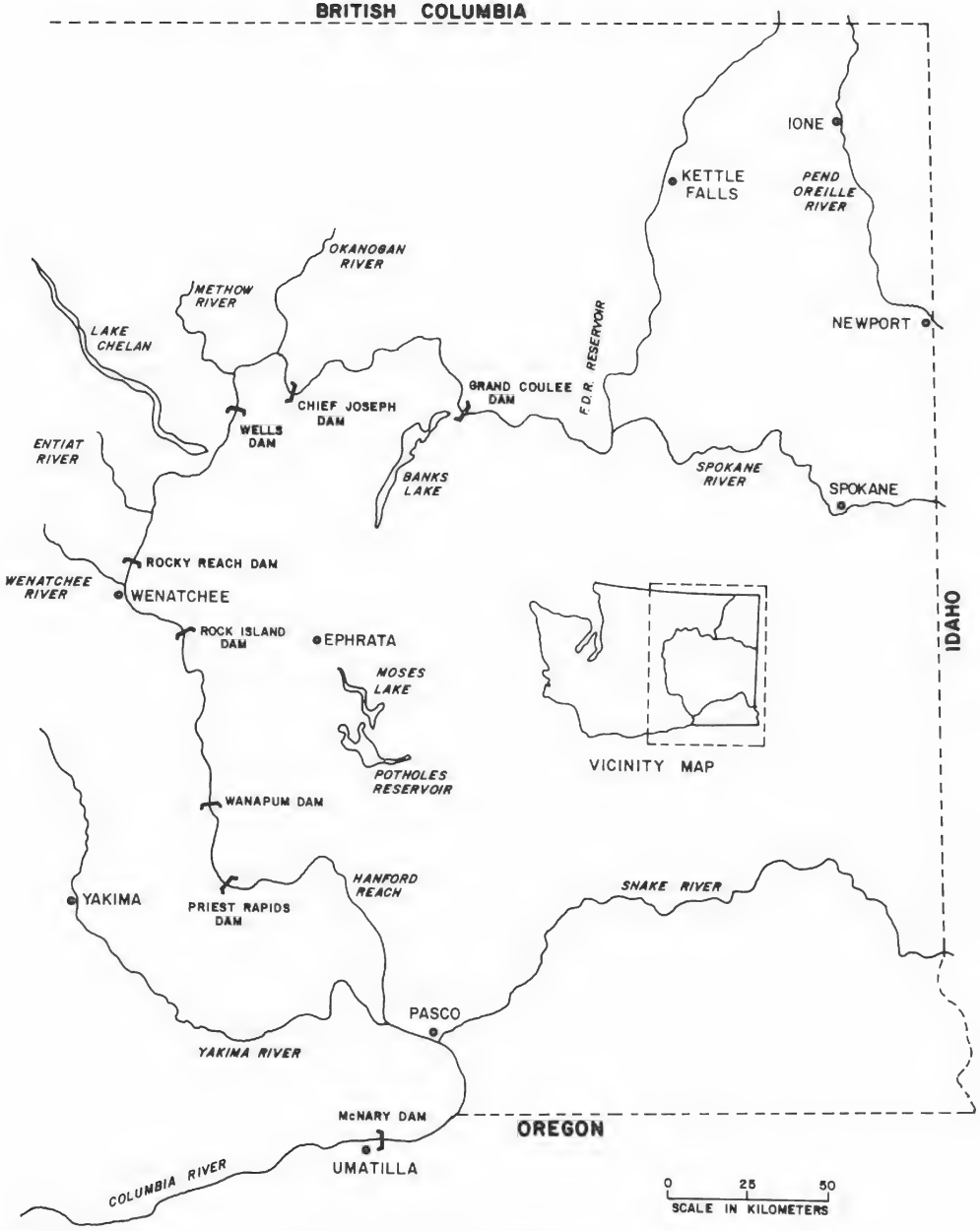

Figure 1. Eastern Washington bald eagle survey area, winters 1974-75 through 1983-84.

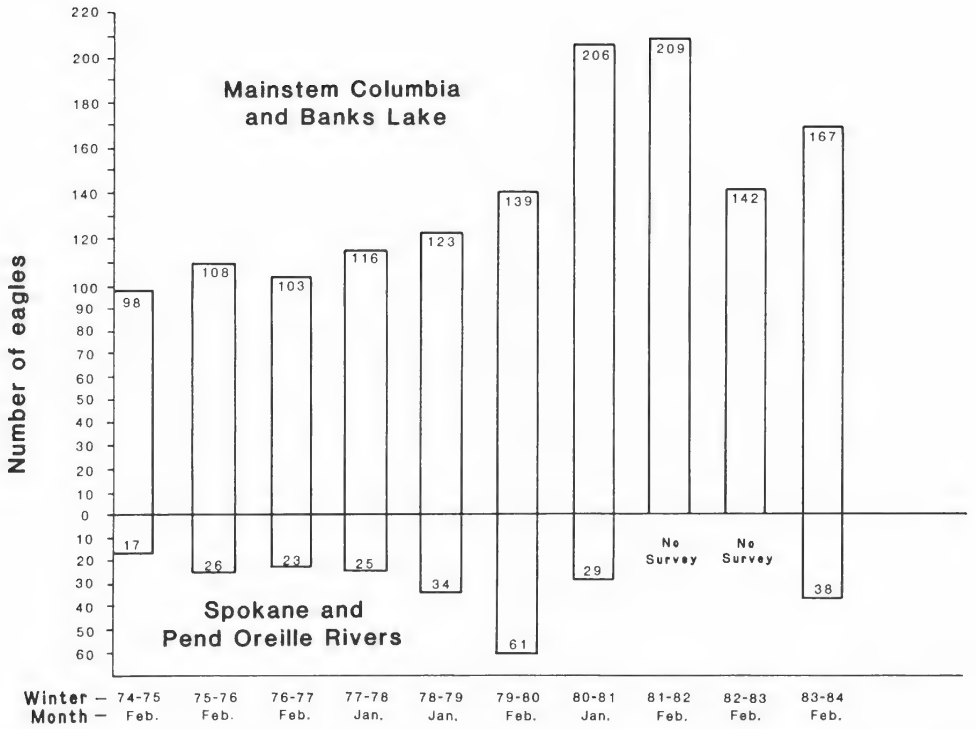

Figure 2. Peak bald eagle counts during aerial surveys along major water bodies in eastern Washington, winters of 1974-75 through 1983-84.

comprised 41 percent of the mainstem Columbia River-Banks Lake shoreline. However, it accounted for only 19 percent, 21 percent, 24 percent, 29 percent and 25 percent of the eagles seen during our surveys for the months of November-March, respectively.

Bald eagles occurred in our eastern Washington survey area at an average of 2.1 adults per subadult (n = 5483). Adult and subadult eagles were not distributed randomly (chi-square calculated = 125.41; tabular value 8 df, 0.05 level of probability = 15.507) throughout the Columbia River-Banks Lake study area (Table 4). Wells Reservoir and the Hanford Reach (Table 4) supported lower ($P < 0.05$) proportions of adults. Banks Lake also supported fewer ($P < 0.05$) adults in December, after which time the lake usually froze over. FDR and Chief Joseph reservoirs supported significantly higher proportions of adults ($P < 0.05$) than the other Columbia River-Banks Lake water bodies (Table 4).

Discussion

Numbers of bald eagles recorded during our surveys doubled between 1975 and 1984. Although Washington's mid-winter bald eagle survey reports have shown an increasing trend since 1979, they present only eagle numbers for early January and reflect varying degrees of survey effort (Knight *et al.* 1980, Millsap 1986). Our data reflect consistent survey methodology over a five-month period during 10 winters. Eagles increased in number during our survey period for each of the five months surveyed. During the winter of 1981-82, eagles wintered further south in the U.S. because of unusually cold temperatures (Millsap 1986), yet we obtained two of our five highest bald eagle counts during this winter, 183 in January and 209 in February.

The increase in eagle numbers within our survey area was influenced by increases along FDR Reservoir and Banks Lake. During late fall, lake whitefish (*Coregonus clupeaformis*) spawning at

TABLE 1. Bald eagle abundance and distribution along the mainstem Columbia River (Pasco to Kettle Falls) and Banks Lake during aerial surveys, winters of 1974-75 through 1983-84.

	1974 -75	1975 -76	1976 -77	1977 -78	1978 -79	1979 -80	1980 -81	1981 -82	1982 -83	1983 -84
November		56	61	58	32	43	48		94	103
December		67	65	83	90	59	175	203	114	185
January	64	99	86	116	123	100	206	183	109	148
February	98	108	103	111	97	139	113	209	142	167
March	71	64	41	80	34	68	74	52		154

[1]Detailed numbers by area are available from the authors upon request.

TABLE 2. Bald eagle abundance along the Spokane and Pend Oreille rivers during aerial surveys, winters of 1974-75 through 1983-84.[1]

	1974 -75	1975 -76	1976 -77	1977 -78	1978 -79	1979 -80	1980 -81	1981 -82	1982 -83	1983 -84
November		5	6	4	8	17	15	NS[2]	NS	7
December		9	7	9	20	26	26	NS	NS	15
January	8	17	9	25	34	20	29	NS	NS	26
February	17	26	23	28	37	61	24	NS	NS	38
March	7	12	18	11	25	31	21	37	NS	40

[1]Detailed numbers by area are available from the authors upon request.
[2]NS indicates no survey.

TABLE 3. Proportion of total bald eagles seen during aerial surveys in comparison to proportion of shoreline length of mainstem Columbia River water bodies.

	Shoreline length		Percent of total bald eagles/water body[1]					
Water body	Km	% of total	Nov.	Dec.	Jan.	Feb.	Mar.	% of Total
FDR Reservoir	335	22	23	28G	26G	28G	31G	27G
Banks Lake	146	10	27G	29G	19G	13G	23G	21G
Chief Joseph Reservoir	206	14	18	10L	15	13	12	13
Wells Reservoir	197	13	13	11	15	18G	12	14
Rocky Reach Reservoir	146	10	4L	5L	5L	7L	7L	6L
Rock Island Reservoir	70	5	1L	1L	2L	2L	1L	2L
Wanapum Reservoir	135	9	4L	4L	5L	7L	6L	5L
Priest Rapids Reservoir	76	5	2L	3	3L	4	4	3L
Hanford Reach	190	13	8L	8L	9L	9L	5L	8L
Totals	1501	100	100	100	100	100	100	100
number of eagles =			495	1031	1234	1287	638	4685
number of surveys =			8	9	10	10	9	46
eagles/survey($\bar{x}$) =			61.9	114.6	123.4	128.7	70.9	101.1
standard deviation =			24.5	56.8	43.9	36.2	34.5	49.5

[1]Significantly greater (G) or lesser (L) proportions of bald eagles ($P < 0.05$) compared to proportion of shoreline length, were determined by methodology described by Nue *et al.* (1974).

TABLE 4. Age ratios (adults/subadult) of bald eagles wintering along eastern Washington water bodies, winters of 1974-75 through 1983-84.

Water body	No. of Eagles	Age ratio (adults:subadult)[1]					Total Age Ratio
		Nov.	Dec.	Jan.	Feb.	Mar.	
FDR Reservoir	1280	3.0	2.9G	3.3G	3.0G	2.6	3.0G
Banks Lake	981	1.6	1.5L	1.7	2.9	3.5	1.9
Chief Joseph Reservoir	614	3.5	3.0G	2.9G	3.8G	3.0	3.2G
Wells Reservoir	667	2.0	1.4	1.5L	1.0L	1.6L	1.3L
Rocky Reach Reservoir	275	1.6	2.1	2.3	3.0	2.8	2.5
Rock Island Reservoir	76	6.1	1.3	1.5	1.9	4.0	1.8
Wanapum Reservoir	250	3.5	1.9	2.0	1.5	2.0	1.8
Priest Rapids Reservoir	155	4.0	1.7	1.8	1.8	2.3	1.9
Hanford Reach	387	1.3	1.0L	1.1L	1.4L	1.7	1.2L
Total	4685	2.2	1.9	2.0	2.1	2.8	2.1
Spokane River	473	1.8	2.7	3.2	2.3	1.8	2.3
Pend Oreille River	325	2.9	2.5	2.4	3.2	2.0	2.5
Total	798	2.3	2.6	2.8	2.5	1.9	2.4

[1]Significantly greater (G) or lesser (L) ratios of adults to subadult ($P < 0.05$) were determined by methodology described by Nue *et al.* (1974).

Banks Lake and an abundant waterfowl population, provided a food source for bald eagles. Bald eagle food habits along FDR Reservoir are unknown.

The use of peak counts may inadequately represent the number of eagles which use an area. Counts at Banks Lake support this concept. During the winter of 1983-84 we tallied only five eagles along the lake during the January survey, but our November and March surveys tallied 51 and 44 eagles, respectively. January, the first half of which is the period of the NWF mid-winter bald eagle survey, accounted for only three of our 10 peak eagle counts. Thus, the NWF bald eagle surveys may inaccurately present eagle abundance and distribution in eastern Washington and underemphasize the importance of some wintering areas.

The non-random distribution of eagles in our survey area (Table 3) may have been influenced by several factors (i.e., food availability, perch sites, and human activity). Anadromous fish were available to bald eagles in significant numbers only along the Hanford Reach (Fitzner and Hanson 1979); however, eagles there also fed heavily on wintering waterfowl (Fitzner *et al.* 1980). Eagle abundance along Banks Lake seemed influenced by food availability (waterfowl, whitefish, and other fish species). After the lake froze, eagle numbers declined sharply. Abundant perch sites along the north half of the lake and relative isolation from human activity may also have attracted wintering eagles.

Ratios of adults to subadults were higher ($P < 0.05$) along FDR and Chief Joseph reservoirs and lower ($P < 0.05$) along Wells Reservoir and the Hanford Reach (areas with abundant waterfowl) (Table 4). Stalmaster *et al.* 1979, Fitzner *et al.* 1980, and Fielder 1982 hypothesized that high proportions of subadults tend to occur in areas with easily available food sources. This generalization seemed true within our study area.

NWF mid-winter bald eagle surveys indicate that subadults comprise a lower proportion (27%) of wintering populations above 38°N latitude and a higher proportion (45%) below that latitude (Millsap 1986). Our eastern Washington survey area included one of the most northern wintering populations of bald eagles in the conterminous 48 states and centers on the 48°N latitude line, well north of 38°N latitude. Subadults comprised 33 percent and 26 percent

of January populations along the Columbia River-Banks Lake and Spokane-Pend Oreille rivers, respectively. In relation to Millsap's conclusion, the Columbia River-Banks Lake area supports a relatively high proportion of subadults.

Bald eagles are protected by the Endangered Species Act (U.S. Dep. Interior 1978). Resource managers and project developers must therefore consider bald eagles during most forms of land and water development projects (i.e., hydroelectric, irrigation, recreational, silvicultural, navigation, residential, and industrial projects). Tables 1 and 2 provide managers and developers a 10 year history of comparable bald eagle abundance information throughout the eagle's wintering period in eastern Washington.

Literature Cited

Fielder, P. C. 1982. Food habits of bald eagles along the mid-Columbia River, Washington. Murrelet 63:46-50.

Fielder, P.C., and R. G. Starkey. 1980. Wintering bald eagle use along the upper Columbia River, Washington. *In* R. L. Knight, G. T. Allen, M. V. Stalmaster, and C. W. Servheen (eds.). Proc. Washington Bald Eagle Symp., The Nature Conservancy, Seattle. Pp. 177-193.

Fitzner, R. E., and W. C. Hanson. 1979. A congregation of wintering bald eagles. Condor 81:311-313.

Fitzner, R. E., W. C. Hanson, D. G. Watson, and W. Rickard. 1980. Bald eagles of the Hanford National Environmental Research Park. *In* R. L. Knight, G. T. Allen, M. V. Stalmaster, and C. W. Servheen (eds.) Proc. Washington Bald Eagle Symp., The Nature Conservancy, Seattle. Pp. 207-218.

Ingram, T. N. 1965. Wintering bald eagles at Guttenberg, Iowa-Cassville, Wisconsin, 1964-65. Iowa Bird Life 35:66-78.

Knight, R. L., T. P. D'Acci and R. C. Friesz. 1980. Summary of the mid-winter bald eagle survey in Washington. *In* R. L. Knight, G. T. Allen, M. V. Stalmaster and C. W. Servheen (eds.). Proc. Washington Bald Eagle Symp. The Nature Conservancy, Seattle. Pp. 123-131.

Received 20 January 1986
Accepted for publication 24 June 1987

Acknowledgements

This research was funded by the U.S. Fish and Wildlife Service, Ecological Services and, during the last two winters, by the Public Utility Districts of Chelan, Douglas, and Grant counties. Barry Keesee, Jim McGee, Bob Perleberg, and Daryll Pock assisted as additional observers on several flights. John Harris prepared the study area map and Carla Warnock typed the manuscript. We are grateful to Dave Carlile for his statistical review of this paper as well as Dick Fitzner and Mark Stalmaster, whose review and comments enhanced earlier drafts of this manuscript.

McClelland, B. R., L. S. Young, D. S. Shea, P. T. McClelland, H. L. Allen, and E. B. Spettigue. 1982. The bald eagle concentration in Glacier National Park, Montana: origin, growth, and variation in numbers. Living Bird 19:133-155.

Millsap, B. A. 1986. Status of wintering bald eagles in the conterminous 48 states. Wildl. Soc. Bull. 14:433-440.

Neu, C. W., C. R. Beyers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. J. Wildl. Manage. 38:541-545.

Spencer, D. A. 1976. Wintering of the migrant bald eagle in the lower 48 states. Nat. Agric. Chem. Assoc., Washington, D.C.

Stalmaster, M. V., J. R. Newman, and A. J. Hansen. 1979. Population dynamics of wintering bald eagles on the Nooksack River, Washington. Northw. Sci. 53:126-131.

Steenhof, K., S. S. Berlinger, and L. H. Fredrickson. 1980. Habitat use by wintering bald eagles in South Dakota. J. Wildl. Manage. 44:798-805.

U.S. Dep. Interior. 1978. Determination of certain bald eagle populations as endangered or threatened. Fed. Reg. 43:6230-6233.

Wood, B. 1980. Winter ecology of bald eagles at Grand Coulee Dam, Washington. *In* R. L. Knight, G. T. Allen, M. V. Stalmaster, and C. W. Servheen (eds.). Proc. Washington Bald Eagle Symp., The Nature Conservancy, Seattle. Pp. 195-204.

Young, L. S. 1983. Movements of bald eagles associated with autumn concentrations in Glacier National Park. University of Montana, Missoula. (M.S. Thesis.)

P. M. Woodard, Department of Forest Science
University of Alberta, Edmonton, Alberta, Canada T6G 2H1

and

Grant Cummins, General Delivery, Summerland, B.C. V0H 1Z0

Engelmann Spruce, Lodgepole Pine and Subalpine Fir Seed Germination Success on Ashbed Conditions

Abstract

In the lodgepole pine, Engelmann spruce, and subalpine fir association, pine seedlings commonly dominate immediately after fire disturbances. To test if this outcome is a response to seed availability or environmental conditions, Engelmann spruce, lodgepole pine, and subalpine fir seeds were germinated under controlled laboratory conditions. Germination beds consisted of ash covered seedbeds and sterile media moistened with one of five different concentrations of soluble ion leachates decanted from ash. One half of the seeds for each treatment were cold stratified (a pregermination treatment where moist seeds are exposed to near freezing temperatures) on one of the five germination seedbeds, while the other half of the seeds were first cold stratified on moist filter paper and then transferred to germination seedbeds. We found that all three species are capable of germinating on burned seedbeds. Lodgepole pine was unaffected by stratification or treatment procedures used. Significant differences in final germination percentages did exist among the five treatments for spruce and fir but these differences were not consistent with relative differences in specific conductance or ion concentrations. Spruce seed germination was significantly improved when seeds were stratified on ashbed conditions. Our results clearly show that the chemical conditions of the ashbed do not favor pine establishment when all three species are subjected to similar conditions.

Introduction

Combustion residue of ash, charred material, and charcoal remain on the soil surface subsequent to the passage of a forest fire. Tree seed germination success is highly influenced by the physical, chemical, and biological properties of this seedbed medium (Thrupp 1939, Tryon 1948, deKeijzer and Hermann 1966, Woodard 1983). The effect of combustion residue on tree seed germination varies by tree species tested and between experiments involving the same species (deKeijzer and Hermann 1966, Woodard 1983). Conflicting results can often be attributed to the research environment (laboratory versus field), type of residue used (ion rich ash versus inert charcoal), or to sampling designs or procedures used. Most previous studies have failed to test the ion concentration effects of ash during the stratification phase of germination (deKeijzer and Hermann 1966, Woodard 1983). The intake of water versus soluble ion (particularly cations) may significantly affect the germination success of certain tree species by affecting the water potential gradient between the leachate and the endosperms at the integument or, perhaps, the enzymatic activity required for cell enlargement and the eventual emergence of the radicle.

The objectives of this study were to: (1) verify the results of Woodard (1983), who showed that lodgepole pine (*Pinus contorta* Dougl.) and Engelmann spruce (*Picea engelmannii* Parry) seed germination was reduced by the soluble chemicals in the combustion residue, although the effect was only statistically significant for pine, and (2) to determine the stage during the germination process when an effect, if any, occurred. In addition, this study tests the chemical effects of combustion residue on subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) seed germination. The information gained from this study might also answer the ecological question of why, after fire, lodgepole pine seedlings dominate on sites once occupied by spruce, fir, and pine. Is it principally due to the high concentration of available pine seed which is released from serotinous cones or to the physical and chemical conditions which exist as a direct or indirect result of burning?

Study design and methods

Lodgepole pine, Engelmann spruce, and subalpine fir seeds were stratified under two different regimes and germinated under controlled laboratory conditions on five different substrates: (1) 30 ml washed combustion residue placed on filter paper and moistened with 80 ml of distilled water (black body effect), (2) filter paper moistened with 80 ml of dilute combustion residue

leachate (4 parts of distilled water: 1 part combustion residue), (3) filter paper moistened with 80 ml of a medium strength combustion residue leachate (2:1), (4) filter paper moistened with 80 ml of a concentrated combustion residue leachate (1:1) and, (5) 30 ml of untreated combustion residue placed on filter paper and moistened with 80 ml of distilled water. The control treatment consisted of germinating seeds of all three species on filter paper moistened with 80 ml of distilled water. The physical conditions common to all treatments consisted of closed 150 mm diameter x 15 mm high petri dishes lined with one layer of Kimpac (a multilayered absorbent batting; marketed by Seedburo Equipment Co.) and covered with two sheets of Whatman No. 1 white filter paper.

One hundred seeds were sown to 20 individual petri dishes for each species. The seeds in half of the dishes (n = 1000 seeds; 10 reps of 100 seeds) and the control treatment were cold stratified on Whatman No. 1 white filter paper and Kimpac moistened with 80 ml of distilled water (Stratification Treatment 1), while the remaining seeds were cold stratified on the same substrates which would eventually serve as germination beds (Stratification Treatment 2). Stratification consisted of cold storing (4°C) seeds in closed petri dishes in sealed plastic bags in the absence of light for 21 days (ISTA 1976). At the conclusion of the stratification treatment, seeds in Stratification Treatment I were transferred to their appropriate germination substrates prior to transfer to the germination chamber. Seeds processed under Stratification Treatment 2 were transferred directly to the germination chamber.

Seedlots[1] were cleaned of debris and light seeds using a North Dakota blower and counted into each dish using an electronic seed counting device. All seeds were x-rayed prior to treatment in an attempt to identify the number of partially full seeds per seedlots thus allowing for correction of final germination percentages.

[1]Engelmann spruce (seedlot number: DB 21-10-5-76-Se) and lodgepole pine (DR 36-12-5-77Pl) seed were provided by the Pine Ridge Forest Nursery, Alberta, Div. of Energy and Natural Resource, Smoky Lake, Alberta; while the subalpine fir seedlot (a mixture of seedlots 2504 and 5107) was provided by the Ministry of Forests and Lands, Seed Center, British Columbia Ministry of Forests and Lands, Duncan, B.C.

Combustion residue seedbeds and leachates were prepared from preburn organic (L, F, H) materials collected from several mixed pine/spruce/fir soils near Hinton, Alberta (53°24'N, 117°37'W). A composite sample of material from all sites was oven-dried at 70°C and burned with the aid of a propane torch under ambient conditions until glowing and smouldering combustion had ceased. The residue consisted of gray ash and chips of charcoal. Leachates were prepared by soaking combustion residue in various amounts of distilled water for seven days prior to suctioning the liquids through a Buchner funnel lined with a Whatman No. 42 filter paper (deKeijzer and Hermann 1966). The washed combustion residue was prepared by rinsing the residue remaining from the preparation of the dilute leachate solution with an additional volume of distilled water equal to 15 times the volume of combustion residue initially used.

Measurements of total ions using electrical conductivity at 22°C and soluble ion concentrations for Ca, Mg, Na, K, S, P using Inductively Coupled Plasma Analysis were determined from solutions of each treatment. The solution used to measure the conductivity and soluble ions present in the concentrated combustion residue was prepared by mixing enough residue with 200 ml of distilled water to make a thick paste. After soaking this mixture for 24 hours the liquid was suctioned through a Buchner funnel lined with Whatman No. 42 filter paper following procedures described by deKeijzer and Hermann (1966). The final rinse from the washed residue treatment and extracts from the other residue leachates were used to test for electrical conductivity and soluble ions. Measurements of specific conductance were performed immediately. Soluble ion concentrations were determined from 20 ml samples of solutions which were preserved for analysis by adding 0.75 ml of concentrated HNO_3 in the samples and then refrigerating (at 4°C) until tests could be performed by the staff at the Northern Forestry Centre, Canadian Forestry Service, Edmonton. The pH and conductivity of the distilled water used in this experiment was 6.9 and 0.005 mS/cm, respectively.

Germination tests were carried out in a controlled environment cabinet following accepted procedures (ISTA 1976). Lodgepole pine and Engelmann spruce were subjected to 8 hours of light at 30°C followed by 16 hours of darkness

at 20°C for a period of 21 days. Subalpine fir was germinated under the same time/temperature/light regime but for a period of 28 days. Light levels in the cabinet ranged from 3,000 lx (unobstructed) to 1500 lx in the center of stacked dishes enclosed in clear plastic bags. Dish positions within stacks and the location of stacks within bags were changed daily in an attempt to eliminate the effect of dish position on germination success. Humidity and moisture regimes were considered favorable for germination success because there was no need to add fluids to any of the treatment dishes throughout the duration of the experiment. Dishes were checked at two-day intervals. Germinants were counted and removed from the dishes when the length of the radicle exceeded four times the length of the seed (ISTA 1976).

The effects of treatment (5 levels), stratification (2 levels) and their interactions were tested by two-way ANOVA. The control group was not included in this analysis due to absence of a control for stratification method 2. Differences among eleven treatment groups (treatment x stratification + control) were tested by one-way ANOVA. To make the variances homogenous, the data were transformed using the arc sin of the square root of the proportion of seeds that germinated before analysis (Steel and Torrie 1980). The Tukey-HSD procedure was used to compare individual means.

Results

Repeated washing of ash with distilled water removed most soluble ions and reduced the specific conductance (Table 1). The highest conductivity readings and ion concentrations were found in solutions prepared from untreated ash or in the concentrated combustion residue leachate while the lowest values were determined for the washed residue treatment. As expected, the concentrated residue and leachate have far more ions than washed ash or diluted solutions. The trends in conductivity and ion concentrations are similar to those reported in previous literature (Muri 1955, Woodard 1983). However, in comparing these results with those from prior studies, the type of plant material ashed and the methods used to obtain these values must be considered.

Total germination was highest for lodgepole pine, followed by spruce and then by fir (Figure 1). The average germination success for each treatment was based on 10 replications of 100 seeds for each species. Information gained by x-raying seeds prior to treatment did not improve the accuracy of these results as we had anticipated. Although we could distinguish between full and partially full seeds on x-rays, we were not able to identify all viable seeds accurately. In addition, corrections for partially full seeds did not measurably enhance differences between means by reducing standard errors. Therefore, results were analyzed on the basis of total germination success for each dish of 100 seeds rather than the number of germinants per number of full seeds.

Lodgepole pine germination success (89%; S.E. = 2%) did not vary significantly among treatments ($p = 0.227$) or stratification procedure ($p = 0.474$). This result was confirmed by the one-way ANOVA procedure. For spruce and fir, where the S.E. was 2 percent for both species, we found

TABLE 1. Electrical conductivity and concentration of some specific ions present in treatment solutions and substrates.

Treatment	Electrical Conductivity at 22°C (mS/cm)	Elements (ppm) Ca	Mg	Na	K	S	P
control	0.200	23	3	15	2	10	0.1
washed residue	0.075	10	2	2	9	1	1.0
dilute leachate	0.990	160	19	8	131	156	0.2
medium leachate	1.530	274	31	15	236	296	0.2
conc. leachate	2.490	526	55	26	346	513	0.3
conc. residue	2.020	878	92	36	541	743	0.4

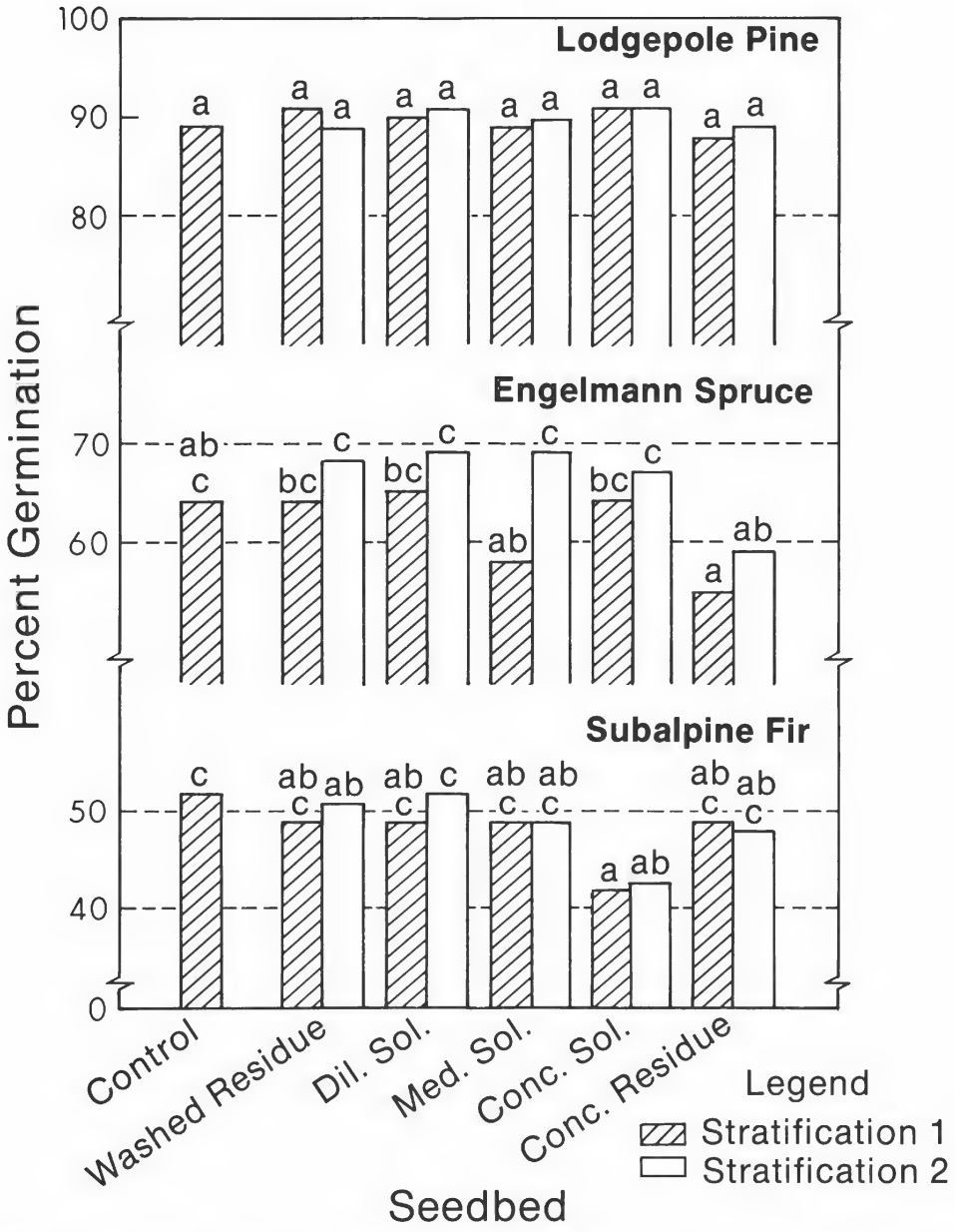

Figure 1. Percent germination by stratification treatment for spruce, pine, and fir seeds sown to a control and five different seedbeds (washed ash residue, concentrated ash residue, and white filter paper moistened with dilute, medium and concentrated ash leachate solutions). Among seedbeds, means identified by the same letter are not significantly different at the 5 percent level.

significant differences among treatments ($p < 0.001$). Stratifying seeds on ash or on substrates moistened with ash leachates significantly and consistently increased spruce germination by 5 percent on average, for all treatments ($p < 0.001$) while for fir the increase was 2 percent but this effect was not significant ($p = 0.234$). The interaction between treatments and stratification methods was not significant for spruce ($p = 0.190$) or fir ($p = 0.853$), indicating the differences between stratification method were constant across the treatments.

The physical and chemical characteristics of the ash or the leachates from the ash had no impact on rate of germination. Well over 90 percent of the total germination for a given species occurred on the same sample day as controls regardless of treatment. Lodgepole pine germinated the fastest (9 days), followed by Englemann spruce (11 days), and subalpine fir (22 days).

Discussion

Statistically significant variation in final germination percentages among treatments do exist for spruce and fir but these results were not consistent with, or directly related to, ion concentrations or conductivity levels determined for leachate solutions or ashbeds. The concentrated leachate solution did significantly reduce the mean total germination for the subalpine fir seedlot when compared to control values, but this response is not consistent with results of other treatments. Also, the fact that seeds of all three species tested germinated better when stratified under the influence of ash or ash leachate further strengthens the conclusion that ash or its characteristics has no detrimental physical or chemical effect on the total germination.

The results of this work are consistent with some previously published data which support the conclusion that ashbeds and their chemical constituents have no effect on tree seed germination success [Fisher 1935 (lodgepole pine), Tarrant 1954 (Douglas-fir), Muri 1955 (Engelmann spruce, subalpine fir), deKeijzer and Hermann 1966 (Douglas-fir), Jarvis 1966 (black spruce, white spruce and jack pine), Sims 1968 (jack pine) and Woodard 1983 (Engelmann spruce)]. However, our results conflict with results from other studies which found ash materials inhibit [Fabricius 1929 (pine, spruce, fir), Tryon 1948 (white pine), Gayle and Gilgan 1951 (lodgepole pine, Douglas-fir), Ahlgren 1959 (black spruce)] or promote tree seed germination [Fisher 1935 (western white pine, Douglas-fir, ponderosa pine, white fir), Herman and Chilcote 1965 (Douglas-fir), Woodard 1983 (lodgepole pine)]. It is difficult to explain the inconsistencies in published results largely because of variations in experimental design and methods, perhaps genetic differences in seedlots, types of residues used, and the limited number of studies pertaining to the species tested. Many previous studies have shown that all of the above factors can influence tree seed germination success. For example, Jeglum (1979) reported that black spruce seed germination on burned feather moss (*Pleurozium schreberi* [*Brid.*] Mitt.) was increased, decreased, or unaffected depending on frequency of watering. Hence, the justification for standard seed testing procedures (ISTA 1976). In this study, all seeds were subjected to identical conditions and the procedures followed are currently accepted by the International Seed Testing Association. Therefore, our approach eliminates most of the variation in environmental conditions which would impact on germination success and confuse the interpretation of our results.

Conclusions

Lodgepole pine seed germination was not significantly affected by the physical or chemical constituents of ash or leachates from ash used in this study. Engelmann spruce and subalpine fir seed germination was affected, but the effect was not consistent or directly related to changes in specific conductance and ion concentrations and the magnitude of these effects was not large enough to be considered ecologically significant. The rate at which germination occurred was not affected by ash or leachates of ash. Although the results of this experiment are only specific to the seedlots used, they do suggest seedbeds covered with ash similar to that used in this study do not favor any one of the three species tested when germination conditions are identical and currently accepted germination procedures are used. Seeds of all species tested were capable of germinating on burned-over seedbeds without reducing the speed of germination or the total number of germinants.

Acknowledgments

Seeds used in this experiment were provided by the Pine Ridge Forest Nursery, Alberta Forest Service and the Duncan Seed Centre, British Columbia Forest Service. We gratefully acknowledge the support and technical assistance of Dr. George Edwards, CFS, Victoria; Dr. Doug Maynard, CFS, Edmonton and Dr. K. Hellum, University of Alberta, Edmonton. Funding for this study was provided through grants from the National Science and Engineering Research Council of Canada and Canadian Forestry Service (Block Grant). Ms. D. Saunders is also acknowledged for her secretarial support.

Literature Cited

Ahlgren, C. E. 1959. Some effects of fire on forest reproduction in northeastern Minnesota. J. For. 57: 194-200.

deKeijzer, S., and R. K. Hermann. 1966. Effects of charcoal on germination of Douglas-fir seed. Northw. Sci. 40:155-163.

Fabricius, L. 1929. The effect of ashes from forest fires upon germination and early development of plants. Forstwissenschaftliches Centralblatt 73:269-276. U.S. For. Serv. Translation No. 14, *By* A. H. Krappe, 1935.

Fisher, G. M. 1935. Comparative germination of tree species on various kinds of surface-soil material in the western white pine type. Ecology 16:606-611.

Gayle, W. B., and W. W. Gilgan. 1951. The effect of slash burning on germination and primary survival of lodgepole pine and Douglas-fir. University of British Columbia, For. Club Res. Note 2, Vancouver.

Hermann, R. K., and W. W. Chilcote. 1965. Effect of seedbeds on germination and survival of Douglas-fir. Oregon State University, For. Res. Lab., Res. Pap. 4.

International Seed Testing Association. 1976. International rules for seed testing. Seed Sci. Technol. 4: 56-119.

Jarvis, J. M. 1966. Seeding white spruce, black spruce and jack pine on burned seedbeds in Manitoba. Can. Dept. Forestry Publ. No. 1166.

Received 4 February 1987
Accepted for publication 24 June 1987

Jeglum, J. K. 1979. Effects of some seedbed types and watering frequencies on germination and growth of black spruce: a greenhouse study. Dept. Environ., Canadian For. Serv. Rep. 0-X-292, Great Lakes For. Res. Cent., Sault Ste. Marie, Ontario, Canada.

Muri, G. 1955. The effect of simulated slash burning on germination, primary survival and top-root ratios of Engelmann spruce and alpine fir. University of British Columbia. For. Club, Res. Note 14, Vancouver.

Sims, H. P. 1968. Effect of water extracts on burned pine duff on germination of jack pine seed. Canada Dept. For. (Rural Development). Bimonthly Res. Notes. 24: 18-19.

Steel, R. G. D., and J. H. Torrie. 1980. Principles and procedures of statistics. 2nd ed. McGraw-Hill Book Company, New York.

Tarrant, R. F. 1954. Soil reaction and germination of Douglas-fir seed. USDA For. Serv. Res. Note 105, Pac. Northw. For. and Range Exp. Sta., Portland, Oregon.

Thrupp, A. C. 1939. Effect of seed-ash characteristics and treatment of seed and soils upon coniferous seed germination. University of Washington, Seattle. Ph.D. Dissertation.

Tryon, E. H. 1948. Effect of charcoal on certain physical, chemical, and biological properties of forest soils. Ecol. Monogr. 18:81-115.

Woodard, P. M. 1983. Germination success of *Pinus contorta* Dougl. and *Picea engelmannii* Parry on burned seedbeds. For. Ecol. Manage. 5:301-306.

Sam C. Saunders, and **Michael E. Moody**
Department of Pure and Applied Mathematics
Washington State University
Pullman, Washington 99164-2930

Great Expectations: or Playing the Odds in the State Lotteries

Abstract

Within the past quarter century there has been a proliferation of state sponsored lotteries in the United States of America. Legislatures regard lotteries as a successful means of imposing a voluntary tax on a citizenry that has become resistant to increased taxation on property, income, sales, or service. Since its introduction in 1982, the Washington State Lottery has returned $300 million to the state general fund. Because by law 40 percent of the total monies wagered must be awarded to the bettors and the same amount to the general fund, an easy calculation gives the total wager by persons in the hope of becoming a millionaire. To evaluate the actual chances of winning using some of the currently accepted betting systems a mathematical model is developed which describes the stochastic behavior of the common state lottery sytems. The model is compared with the classical occupancy problem, from which asymptotic results are derived for the distribution of the number of jackpot winners. Results for the expected number of repeated numbers in successive lotteries are computed as a means of checking the touted betting strategy of playing "hot" numbers. The true expected value of the lottery is determined, and the results are compared with data from the Washington State Lottery. It is found that:

1. As the jackpot increases, the expected return does not significantly change because increased participation raises the likelihood of multiple winners with the payoff split among them.
2. The pattern and cluster systems do not offer a basis for increased expectation of success because the winning combination is itself randomly generated (and carefully monitored) and thus the sequence of winning numbers will obey the unintuitive laws of probability and not those of some "system."
3. The observed persistence of winning numbers is an expected artifact of true random number generation; but which numbers will be repeated cannot be known beforehand so does not offer any basis for making predictions.
4. Our results on expectation may not be persuasive to those individuals whose personal utility function is convex, instead of linear, that is a person for whom a few dollars spent on lottery tickets means virtually nothing.
5. Our results should not be regarded as moralistic fervor against play, since the lottery is fairly run, its participation is voluntary, and it has a higher expected return than many other gambling games with which it competes.

Introduction

The first modern state-sponsored lottery was initiated in New Hampshire in 1964. It proved to be so successful that, as of 1986, twenty-two states, and the District of Columbia, have instituted lotteries which now generate about $16 billion in business annually. Herein we shall concentrate principally upon the Washington state game, *Lotto,* although our results also apply to similar lotteries, such as in New York, Oregon, Maryland, or Delaware where the prizes are split among the winners.

The *Lotto*-style games are played as follows: For a fee (usually $1) the player selects two six-number combinations without repetitions from the first μ whole numbers. The value of μ is adjusted to the population of the state; in New York $\mu = 48$, in Washington $\mu = 44$, in Oregon 42, in Maryland 40, while in Delaware $\mu = 30$. Thus in any lottery of this type there are

$$m = \binom{\mu}{6} = \frac{\mu!}{6!(\mu-6)!}$$

different combinations possible. In Washington $m = 7{,}059{,}052$ and in New York $m = 12{,}271{,}512$. Each week the State randomly selects the winning combination. In Washington's *Lotto* game the largest jackpot is shared equally by all persons selecting winning combinations; a smaller jackpot is shared by all who have selected 5 out of the 6 and another is shared by those selecting 4 of 6. In all of these games the salient feature is that the jackpots accumulate if not won, and thus there is, intermittently, an extremely large jackpot which invariably draws increased participation from among the betting citizens. For example, in Washington on March 1, 1986 there was an $8.5 million jackpot that was shared by two winners. The previous jackpot, which started growing on February 8, 1985, was not won at $1 million; there was no winner the

following week so the prize rose to $2 million; there was no winner the next week (new jackpot $4 million) and the jackpot then increased to $8.5 million which was then claimed by two winners. Since the introduction of the current version of *Lotto* there have been, as of this writing, 37 weeks without winners out of 62 weeks of play, and 8 of the 25 times the jackpot has been won it was shared by at least two winners.

As with many stochastic games, it is quite easy to arrive at erroneous or naïve expectations for one's prospects. This is not surprising since frequently probabilistic behavior will test the intuition of even the trained investigator. For example, the fact that many of the larger state lottery jackpots have been claimed by multiple winners has been observed by many players of the lottery. A person of our acqaintance, who recently won about $1000, gives the following advice:

> Pick an unusual number combination, one that someone else will not likely select. Thus, if you win, you will not have to divide the prize.

The reasoning is that the winning number will be chosen at random and you are equally likely to win whether you have chosen an unusual combination or not. Thus if you follow this advice your expected winnings will be higher. However, we are left with the difficulty of identifying "unusual" numbers.

Although the "systems" employed by individuals are undoubtedly numerous and to lesser or greater degrees inventive, perhaps the best known advocate of a systematic approach to better the odds is Gail Howard of New York. She is a former stock broker and commodities trader, who at one time was among the nation's top commodities forecasters. Her system (marketed in several publications[1]) consists of monitoring "hot" numbers, and by tracking "randomness which forms patterns that are predictable to a certain extent." In many respects her approach to the lottery is much the same as that of an economic forecaster. She claims to "ferret-out" winning numbers by charting the past numbers which have won (*Washington Times.* August 12, 1986, Section B, Page 1):

> About half of all winning numbers have hit within the previous three games; about two-thirds of all winning numbers have hit within the previous five games; and about 87 percent of all winning numbers have hit within the last ten games. So if you play recent winning numbers you increase your chances of winning.

In a recent year, it is reported (*loc. cit.*) that she won 72 second and third place prizes in the various lotteries using her strategy. However, it was not reported how the prizes were distributed between the two places, nor how much was invested to have acquired such a record.

One of the purposes of this note is to analyze some of these popular strategies from a probabilistic framework. We also point out that the frequent accumulation of large jackpots shared by multiple winners, although perhaps not intuitive, is in fact to be expected. Further, we calculate the expected fraction of time there will be no winner or multiple winners in each drawing as a function of the level of participation. The expected fraction of winning numbers that will have been repeated in preceding drawings is also determined, and compared to Howard's empirical evidence. Finally, we utilize all this information and calculate the true expected value of the lottery to a player, and then formulate this into the best advice possible to increase one's expected return.

Expected Return

Whether to play a game of chance and risk losing one's bet should depend upon the expected payoff of the game. This is, of course, related to the odds of winning and the system of rewards. In the Washington *Lotto* two 6-number combinations are selected for each $1 ticket, either of which has the same chance of matching all 6 numbers; it is

$$p_6 = \binom{44}{6}^{-1} \doteq 1.417 \times 10^{-7}.$$

For comparison this is about the same chance as getting a straight-flush followed by three-of-a-kind in two successive hands at poker; or of obtaining heads on each of 23 consecutive tosses of a fair coin; or of getting 11 of 13 spades in a hand of bridge. None of these will occur frequently.

Prizes are also given for matching 5 out of 6, 4 out of 6 and two free Lotto tickets are given

[1]Mrs. Howard offers at least two publications giving advice on how to play the state lotteries. Among her offerings are: *Lottery Buster,* and for the Canadian lottery, *Lottery Advantage.* Her many articles (e.g., Howard, 1984; 1985a,b) are also illuminating. She is the most prominent lottery forecaster, and many tens of thousands of individuals subscribe to her methodology.

if one matches 3 out of 6. Using the hypergeometric probabilities we calculate

$$p_5 = \binom{6}{5}\binom{38}{1}/\binom{44}{6} \doteq \frac{1}{30961},$$

$$p_4 = \binom{6}{4}\binom{38}{2}/\binom{44}{6} \doteq \frac{1}{670},$$

$$p_3 = \binom{6}{3}\binom{38}{3}/\binom{44}{6} \doteq \frac{1}{42}.$$

However the amount to be won in each category varies from week to week, at the discretion of the Gaming Commission, depending upon the outcome of the preceding week's lottery. Let us assume some typical values, namely that the payoff is \$1 million, \$750, and \$30, respectively for 6, 5, and 4 matches. Since in Washington's *Lotto* each dollar purchase yields two 6-number combinations, the value (or expected payoff) v of the game must satisfy the equation

$$2(10^6 p_6 + 750p_5 + 30p_4 + vp_3) - 1 = v, \qquad (1)$$

assuming, for simplicity, that the value in the next game will be the same as in the present one. Performing the arithmetic yields $v = -0.655$ in dollars. Thus for each dollar spent the expected loss is about 65 cents. Remember that in a fair game the expected loss is, by definition, zero. But if the grand prize increases, to \$3 million, the value becomes positive. If we were to scale each prize by 3 in eqn. (1) we obtain the value to be $v = \$1.34$.

If the jackpot value becomes large, say to \$8 million, not taking into account any other payoff, one sees the value would be

$$8 \times 10^6(2.83 \times 10^{-7}) - 1 = \$1.26.$$

We might conclude from this calculation that, even though the chance of winning is slight, the game is nonetheless advantageous: the more one bets the more one expects to win. Thus, the odds would seem to favor the players whenever the pot becomes large!

This simple, and erroneous, reasoning seems to be at least partially responsible for the vastly increased participation in *Lotto* whenever the jackpot reaches about \$3 million. However, one's enthusiasm, regardless of how large the prize, should take into account:

- except in the Canadian lottery, the present value of the prize is only about half the nominal value since it is paid in an annuity over 20 years, and
- it is more likely, as participation increases, that the prize will be split among several winners thus reducing the value of the pot to each winner.

The exact mathematical calculation of this last contingency is difficult, and is necessary for a true appraisal of the expected gain to a *Lotto* player. We will return to this point after developing an accurate mathematical model for the game.

A Mathematical Model for *Lotto*

Consider all different number combinations possible in a state lottery as *cells* numbered 1, 2, ... , m. Assume that one of these cells is chosen at random with each purchase of a lottery ticket. These numbers are chosen with replacement, i.e. a given number combination has the same probability of being chosen at each successive drawing whether previously selected or not. This is certainly the case for the player who uses the pseudo-random numbers generated by machine through the method called *Fast-Pic* in Washington or analogous systems elsewhere. There are, to be sure, a number of players who bet "lucky" numbers, birthdays, hunches, etc. which, strictly speaking, may not be random, but this percentage is small and their selections are not likely to vitiate our assumption of randomness.

If this assumption is true then playing a lottery is exactly analogous to tossing a ball at random into one of m cells, each one of which has the same probability of being selected. To calculate the probability that a certain number of cells remain empty after a given number of balls have been so distributed is a difficult combinatorial exercise known as the *Classical Occupancy Problem* (Feller, 1968).

Let X_0 denote the random number of empty cells when n balls have been tossed into m cells. (X_0 corresponds to the number of combinations that have not been selected by any lottery player.) The exact distribution of X_0 is derived in Feller *loc. cit.* It is given for $k = 0, 1, \ldots, n$ by

$$\Pr[X_0 = k] \equiv p(k : n, m) = \binom{m}{k} \sum_{j=0}^{m-k} \binom{m-k}{j} \left(\frac{m-k-j}{m}\right)^n. \qquad (1)$$

Unfortunately this probability is neither simple nor computationally tractable except for very small n, m.

However an ingenious partial result on both the expected value and the asymptotic behavior of X_0 was given by R. von Mises (1939), who reasoned as follows: If n balls are tossed into m cells some of the cells will have no balls in them, some one, some several. We say a cell has i-

occupancy if it contains i balls, for $i = 0,1,\ldots, n$. Let X_i denote the random number of cells with i-occupancy. Now it is clear that

$$\sum_{i=0}^{n} X_i = m, \quad \text{the number of cells} \tag{2}$$

and

$$\sum_{i=0}^{n} iX_i = n, \quad \text{the number of balls.} \tag{3}$$

Consider the indicator variable

$$X_{ij} = \begin{cases} 1 & \text{if the } j^{th} \text{ cell has } i \text{ occupants} \\ 0 & \text{otherwise.} \end{cases} \tag{4}$$

Now $X_i = \sum_{j=1}^{m} X_{ij}$. Consider the number of balls in the first cell. After n tosses have been made this number will be a binomial random variable since each toss has the same probability, *viz.* $1/m$, of going in the first cell. Thus from the definition

$$\Pr[X_{i1} = 1] = \binom{n}{i}\left(\frac{1}{m}\right)^{i}\left(1 - \frac{1}{m}\right)^{n-i}, \quad i = 0, 1, \ldots, n. \tag{5}$$

By symmetry each cell has the same probabilistic behavior and so by (4) and (5)

$$\mathrm{E}[X_i] = m\mathrm{E}[X_{i1}] = m\Pr[X_{i1} = 1] = m\binom{n}{i}\frac{(m-1)^{n-i}}{m^n}. \tag{6}$$

If we define the *factorial polynomial* of degree r for any variate x as

$$(x)_r = \prod_{j=1}^{r}(x + 1 - j) \tag{7}$$

then it becomes possible, by a somewhat more involved argument given by von Mises *loc. cit.*, to obtain the general r^{th} factorial moment of X_k,

$$\mathrm{E}[(X_k)_r] = \frac{(m)_r n!(m-r)^{n-rk}}{(n-rk)!(k!)^r m^n} \tag{8}$$

for n, k, r non-negative integers such that $n \geq rk$, $r \leq m$. The distribution of X_k for $k \geq 1$ is known; it is given in [5], but is quite complicated (like that of X_0), and suffers from the same computational difficulty.

Now, for example, we can easily obtain the mean and variance of X_0, namely,

$$\mathrm{E}[X_0] = m\left(\frac{m-1}{m}\right)^n \tag{9}$$

and

$$\begin{aligned} \mathrm{Var}[X_0] &= \mathrm{E}[(X_0)_2] + \mathrm{E}[X_0] - (\mathrm{E}[X_0])^2 \\ &= \mathrm{E}[X_0]\left[1 + (m-1)\left(\frac{m-2}{m-1}\right)^n - m\left(\frac{m-1}{m}\right)^n\right]. \end{aligned} \tag{10}$$

The asymptotic distribution of X_0 was found by von Mises (1939) under certain conditions, Theorem 1 *If m, $n \to \infty$ so that $me^{-n/m} \to \lambda$ (finite) then the distribution of X_0 becomes, in the limit, a Poisson distribution with mean λ, i.e., for any* $k = 0,1, \ldots$

$$p(k : n, m) - \frac{e^{-\lambda}\lambda^k}{n!} \to 0. \tag{11}$$

Thus for large values of m, n for which $me^{-n/m}$ is moderate the distribution of X_0 can be adequately approximated by a Poisson distribution. Table 1 (after Feller, 1968) displays the approximation.

But if we are interested in the probability that $X_0 = 0$ for other values of m, n then (1) gives

$$p(0 : n, m) = \sum_{j=0}^{m}(-1)^j\binom{m}{j}\left(\frac{m-j}{m}\right)^n. \tag{12}$$

TABLE 1. Poisson Approximation to $p(k : n, 1000)$, the Probabilities of Finding Exactly k Empty Cells When n Balls are Randomly Distributed Into 1000 Cells

		$p(k : n, 1000)$							
		k							
n	λ	0	1	2	3	5	7	9	11
5000	6.74	0.0012	0.0080	0.0269	0.0604	0.1371	0.1482	0.0935	0.0386
5500	4.09	0.0167	0.0685	0.1400	0.1909	0.1596	0.0636	0.0148	0.0023
6000	2.48	0.0838	0.2077	0.2575	0.2128	0.0655	0.0096	0.0008	
6500	1.50	0.2231	0.3347	0.2510	0.1255	0.0141	0.0008		
7000	0.91	0.4027	0.3661	0.1666	0.0506	0.0021			
7500	0.55	0.5777	0.3163	0.0873	0.0162	0.0003			
8000	0.34	0.7126	0.2406	0.0414	0.0049				
8500	0.20	0.8187	0.1637	0.0164	0.0011				
9000	0.12	0.8869	0.1064	0.0064	0.0003				

This calculation is not feasible even by machine for n, m very large. Notice that if $n = m \ln(m/\lambda)$ as $m \to \infty$ then not only does

$$m\left(\frac{m-1}{m}\right)^n \to \frac{\lambda^k}{k!} \quad \text{but also} \quad p(0:n,m) \to e^{-\lambda}$$

since

$$\binom{m}{k}\left(\frac{m-k}{m}\right)^n \to \frac{\lambda^k}{k!} \quad \text{as } m \to \infty.$$

But in the circumstance that $m \to \infty$ with $\nu = n/m$ fixed then each term of (12), except the first, diverges. A simple method of calculating this probability is yet to be found in this case.

Unfortunately the von Mises criterion cannot always be realistically met for lotteries. Consider the case in the New York lottery where $m \doteq 1.2 \times 10^7$ and $n \doteq 2 \times 10^7$; then $\lambda \doteq 2.27 \times 10^5$, an impractical value for a Poisson approximation. Moreover in all state lotteries convergence is appropriately modelled by

$$n = m\nu \quad \text{for some fixed } \nu \text{ as } m \to \infty, \tag{13}$$

in which case the distribution of X_0 does not converge to a Poisson. However, this is not the impression conveyed by Feller, *loc. cit.*, (p. 105)

> In practice we may use the (Poisson as an) approximation whenever (our number) m is great; for moderate values of m an estimate of the error is required . . . but we shall not enter into it.

One might conclude this if one only examined eqn. (9), since for m as small as 10, $\mathrm{E}[X_0] \doteq me^{-n/m}$ for any value of n; but examining eqn. (10) one sees otherwise. We state

Theorem 2 *If $\nu = n/m$* is fixed for n,m large then

$$\mathrm{E}[X_0] \cong me^{-\nu} \tag{14}$$

and

$$\mathrm{Var}[X_0] \cong me^{-\nu}(1-(1+\nu)e^{-\nu}). \tag{15}$$

Proof: The first claim is obvious since under these conditions

$$\lim_{m\to\infty}\left(\frac{m-1}{m}\right)^{m\nu} = e^{-\nu}.$$

From eqn. (10) the quantity in square brackets becomes

$$\begin{aligned}[\cdots] &= 1-\left(\frac{m-1}{m}\right)^n\left[m-(m-1)\left(1-\frac{1}{(m-1)^2}\right)\right] \\ &= 1-\left(1-\frac{1}{m}\right)^n\left\{1+(m-1)\left[1-\left(1-\frac{1}{(m-1)^2}\right)^n\right]\right\}. \end{aligned} \tag{16}$$

By setting

$$m-1 = \frac{1}{t}, \quad \kappa(t) = \nu\left(1+\frac{1}{t}\right),$$

the term in curly braces in eqn. (16) becomes in the limit

$$\lim_{m\to\infty}\{\cdots\} = 1+\lim_{t\downarrow 0}\left[\frac{1-(1-t^2)^{\kappa(t)}}{t}\right]. \tag{17}$$

Applying L'Hopital's rule in (17) and using the expansion $-\ln(1-t^2) = t^2 + o(t^2)$ we infer

$$\lim_{t\downarrow 0}[\cdots] = \lim_{t\downarrow 0}\left[\frac{2t\kappa(t)}{1-t^2} - \kappa'(t)\ln(1-t^2)\right] = \nu,$$

which gives the result claimed. ■

For the distribution of X_0 to converge to the Poisson it is necessary that the variance converge to the mean and we see in this circumstance that it will not. But the case $\nu = n/m$ fixed for n,m large is exactly the case we are interested in when we consider state lotteries. We note that virtually nothing more than the moments of X_k for $k \geq 1$, as given in eqn. (8), is known about the exact distribution, since computation is so difficult.

Let us normalize X_k by considering $U_k = X_k/m$, the fraction of cells having k-occupancy among the m. Let $\nu = n/m$ be the fraction of tickets sold per combination, called the *relative participation*. From eqn. (6) we then see, as $m \to \infty$, that

$$\mathrm{E}[U_k] = \left(\frac{m-1}{m}\right)^n \frac{\nu^k}{k!}\prod_{j=1}^{k}\left(\frac{1+\frac{1-j}{m\nu}}{1-\frac{j}{m}}\right) \to \frac{e^{-\nu}\nu^k}{k!}. \tag{18}$$

These asymptotic values yield an obvious interpretation with eqn. (2) and (3).

Moreover, one may check that

$$\mathrm{Var}[U_k] \to 0 \quad \text{as } m \to \infty.$$

We display this convergence for $k = 2$, $\nu = 2$ in Table 2.

TABLE 2. The variance of U_2 for various m and $\nu = 2$

m					
10	10^2	10^3	10^4	10^5	10^6
3.373×10^{-2}	4.089×10^{-3}	4.164×10^{-4}	4.171×10^{-5}	4.172×10^{-6}	4.172×10^{-7}

We assert that for realistic values of n and m in a state lottery the random U_k are virtually deterministic, and for all practical purposes the fractions

$$\rho_k(\nu) \equiv \mathrm{E}[U_k] \doteq \frac{e^{-\nu}\nu^k}{k!} \quad \text{with } \nu = \frac{n}{m} \tag{19}$$

give the probability there will be k winners sharing the grand prize in the lottery as a function of ν. This behavior is illustrated in Table 3 for a typical value of the relative participation $\theta = 3/2$:

TABLE 3. The expected proportion for various occupancy numbers, $\nu = 1.5$.

Occupancy number (k)	0	1	2	3	≥ 4
Expected proportion ($\mathrm{E}[U_k]$)	0.223	0.335	0.254	0.126	0.065

Thus if the *Lotto* game sells $n = 10.5$ million tickets for which $m = \binom{44}{6} \doteq 7 \times 10^6$ combinations are available, *there is nearly 1 chance in 4 that no person will obtain a 6-match and win the jackpot.* This seems surprisingly high to most people.

Usually fewer tickets are sold; suppose only 3.5 million. Then we have $\nu = 1/2$ and Table 4 reveals that there is now a 60 percent chance of no jackpot winner.

TABLE 4. Expected proportion when $\nu = 0.5$.

Occupancy number (k)	0	1	≥ 2
Expected proportion ($\mathrm{E}[U_k]$)	0.607	0.303	0.09

To see the behavior of the probability of various multiplicities as a function of the betting participation ν we plot in Figure 1 ϱ_0, ϱ_1, and ϱ_+

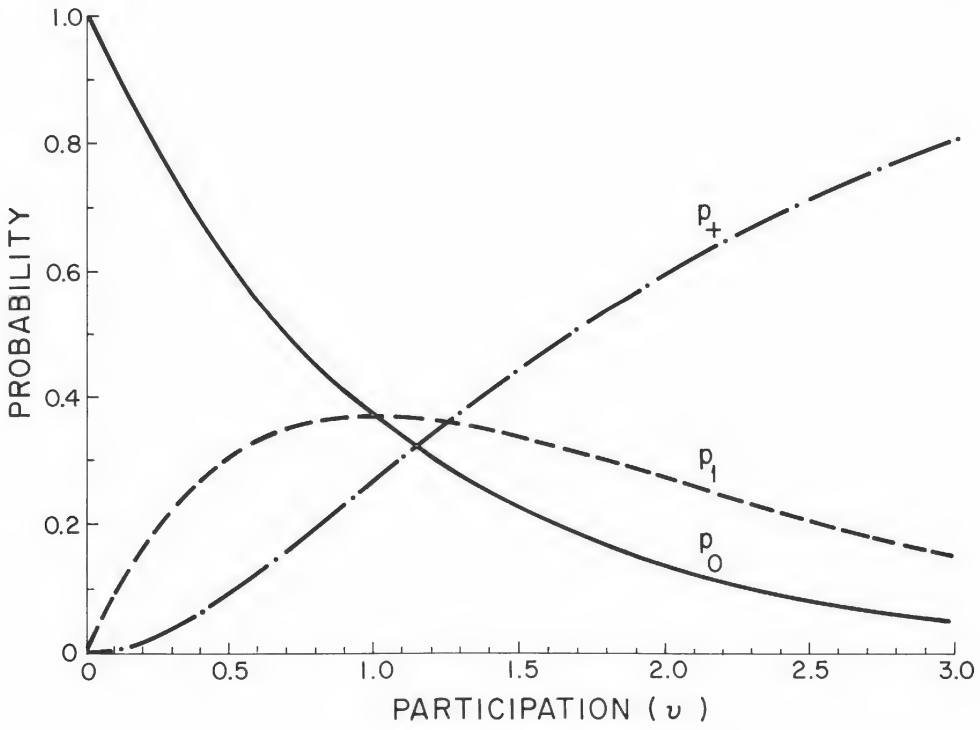

Figure 1. The probability of no winner (ϱ_0), exactly one winner (ϱ_1) or multiple winners ($\varrho_+ = \varrho_2 + \varrho_3 + \cdots$), versus the relative participation θ. The probability that there is no winner, so that the jackpot increases, is surprisingly high even with large relative participation.

$= \varrho_2 + \varrho_3 + \cdots$ (the chance of multiple winners of the jackpot).

The Persistence of Winning Numbers

As we have noted, Howard's system is based upon the empirical claim that certain numbers among those that have been chosen as winning lottery combinations remain "hot": these numbers reoccur with extraordinarily high frequency, far beyond what could be explained by a random model. Some of her startling empirical frequency records have been previously quoted.

We will now show, surprisingly enough, that the fractions she gave are in virtual accord with the predictions of a probabilistic model for the percentage of reoccurrences *of one particular state lottery.* (Although the state upon which her data is based is not specified, such data clearly could not be true for all lotteries independent of μ.)

The winning combination is a subset of size $\zeta = 6$ drawn at random without replacement (by State authorities) from the set of the first μ natural numbers. Recall that the number of such combinations is $m = \binom{\mu}{6}$. Assume that winning combinations are drawn repeatedly for $\omega \geq 1$ times. Label these sets of winning numbers $W_1,\ldots,W_\omega$, and record the *span* $K_\omega = \cup_{i=1}^{\omega} W_i$, the set of all different winning numbers obtained in the first ω weeks. A final winning combination, say W_0, is drawn. The repeated set is

$$R = W_0 \cap K_\omega,$$

i.e. the set of numbers in the final winning combination that have appeared in the preceding ω week's drawing. We ask for the expected value of the size of R, call it $R^{\#}$. (Here $R^{\#}$ means the cardinality of the set.) By the theorem on conditional expectations

$$\mathrm{E}[R^{\#}] = \mathrm{E}\left\{\mathrm{E}[R^{\#} \mid K_\omega^{\#}]\right\}, \tag{1}$$

and a little reasoning shows that

$$\Pr[R^{\#} = r \mid K_\omega^{\#} = k] = \binom{k}{r}\binom{\mu-k}{\zeta-r}\Big/\binom{\mu}{\zeta}.$$

This is a hypergeometric distribution which has known means $\zeta k/\mu$. Hence the conditional expectation in eqn. (1) is

$$\mathrm{E}[R^{\#} \mid K_\omega^{\#}] = \frac{\zeta K_\omega^{\#}}{\mu}. \tag{2}$$

Now consider the random set $K_\omega = K_{\omega-1} \cup W_\omega$, and thereby the conditional random variable defined by

$$[K_\omega^{\#} \mid K_{\omega-1}^{\#} = k_{\omega-1}] = k_{\omega-1} + k \quad \text{w.p.} \quad \binom{k_{\omega-1}}{\zeta-k}\binom{\mu-k_{\omega-1}}{k}\Big/\binom{\mu}{\zeta}.$$

By taking expectations we have

$$\mathrm{E}[K_\omega^{\#} \mid k_{\omega-1}] = k_{\omega-1} + \frac{\zeta}{\mu}(\mu - k_{\omega-1}) = \zeta + k_{\omega-1}\left(1 - \frac{\zeta}{\mu}\right).$$

By analogy we have for $j = 0,\ldots,-2$

$$\mathrm{E}[K_{\omega-j}^{\#} \mid k_{\omega-j-1}] = \zeta + k_{\omega-j-1}\left(1 - \frac{\zeta}{\mu}\right).$$

Thus by iteration

$$\begin{aligned}\mathrm{E}[K_\omega^{\#} \mid k_{\omega-2}] &= \zeta + \left(1 - \frac{\zeta}{\mu}\right)\left[\zeta + k_{\omega-2}\left(1 - \frac{\zeta}{\mu}\right)\right] \\ &= \zeta + \zeta\left(1 - \frac{\zeta}{\mu}\right) + k_{\omega-2}\left(1 - \frac{\zeta}{\mu}\right)^2.\end{aligned}$$

Continuing in like manner we have

$$\mathrm{E}[K_\omega^{\#} \mid k_{\omega-(\omega-1)}] = \zeta \sum_{j=0}^{\omega-2}\left(1 - \frac{\zeta}{\mu}\right)^j + k_1\left(1 - \frac{\zeta}{\mu}\right)^{\omega-1}$$

and after simplification we find the conditional expectation to be

$$\mathrm{E}[K_\omega^{\#} \mid K_1^{\#}] = \mu\left[1 - \left(1 - \frac{\zeta}{\mu}\right)^{\omega-1}\right] + K_1^{\#}\left(1 - \frac{\zeta}{\mu}\right)^{\omega-1}.$$

But since $\mathrm{E}[K_1^{\#}] = \mathrm{E}[W_1] = \zeta$, we obtain for the unconditional expectation

$$\mathrm{E}[K_\omega^{\#}] = \mu\left[1 - \left(1 - \frac{\zeta}{\mu}\right)^{\omega-1}\right] + \zeta\left(1 - \frac{\zeta}{\mu}\right)^{\omega-1}.$$

Hence from (2), after simplification, we have the remarkably simple result which we state in

Theorem 3 *A sample of size ζ is drawn without replacement from the set of the first μ natural numbers. This is repeated $\omega + 1$ times. The set of repeated numbers is R, i.e. the set of numbers in the last sample which had occurred in the preceding ω samples. The number of elements in R is called $R^{\#}$ and it has the expectation*

$$\mathrm{E}[R^{\#}] = \zeta\left[1 - \left(1 - \frac{\zeta}{\mu}\right)^{\omega}\right] \doteq \zeta\left[1 - e^{-(\zeta\omega/\mu)}\right]. \tag{3}$$

This method of derivation actually yields the distribution of $R^{\#}$, more than is required for the expectation. But from the simplicity of $\mathrm{E}[R^{\#}]$, as shown in (3), an easy explanation presents itself. The expectation is merely the sample size ζ times the probability of any fixed fraction ζ/μ not being covered in ω independent trials.[2] We have the immediate

Corollary 1 *If the samples of size ζ are drawn with replacement for $(\omega + 1)$ times, the expected number of repetitions in the last sample among the preceding ω is*

$$\mathrm{E}[R^{\#}] = \zeta\left[1 - \left(1 - \frac{1}{\mu}\right)^{\zeta\omega}\right] \doteq \zeta\left[1 - e^{-(\zeta\omega/\mu)}\right].$$

In order to see the values of the fraction of repetitions we tabulate $\mathrm{E}[R^{\#}/\zeta]$ for various ω and μ with $\zeta = 6$ in Table 5.

---

[2] The authors are indebted to a referee for this observation.

TABLE 5. The fraction of repetitions with $\zeta = 6$.

	μ	ω = 3	4	5	6	10	11	15
NY	48	0.330	0.414	0.487	0.551	0.737	0.769	0.865
WA	44	0.356	0.444	0.519	0.585	0.769	0.801	0.889
OR	42	0.370	0.460	0.537	0.603	0.786	0.817	0.901
MD	40	0.386	0.478	0.556	0.623	0.803	0.833	0.913
VT	38	0.403	0.497	0.577	0.643	0.821	0.849	0.924
DE	30	0.488	0.590	0.672	0.738	0.893	0.914	0.965

Thus for any state with $\mu \leq 38$, as it was formerly in Oregon, the expected persistence of winning numbers agrees with sufficient accord with the empirical fractions reported by Howard *loc. cit.* But they do not agree so closely with states with $\mu > 38$. However, whatever the state, it is clear that the information gleaned from charting the behavior of past winning combinations cannot be used to better one's odds of winning. By analogy, sequentially and independently tossing a fair coin naturally leads to runs of heads and tails; but the observation of a run of heads will not lead us reasonably to expect that the chance of a head will be anything other than one-half on any future toss.

The True Expectation of the *Lotto* Player

We will now compute the expected gain of a player taking into account the increased chance of multiple winners with higher relative participation. Let us assume that if the jackpot for a particular week's lottery has a present value of P dollars the ensuing relative participation will be ν, *i.e.*, sales of $n = \nu m$ tickets. We opine that ν will generally increase with P. Indeed, this is observed. Here, for simplicity, we shall be concerned only with the jackpot, which in *Lotto* is usually about 10 times the amount shared among 5-match and 4-match winners.

The probability that a particular ticket will be a 6-match winner of the jackpot is $p_6 = 1/m$. Given that this ticket is a winner, its owner's share of the prize will depend upon the occupancy of that number combination by the other players. If their play results in k-occupancy, the fraction of possible combinations of which is given by eqn. III(18), then with probability $e^{-\nu}\nu^k/k!$ the share will be $P/(k+1)$. Hence the player's expected share of the prize is

$$\frac{1}{m}\sum_{k=0}^{\infty}\frac{P}{k+1}\frac{e^{-\nu}\nu^k}{k!} = \frac{P}{m\nu}(1-e^{-\nu}). \tag{4}$$

Thus we have

Theorem 4 *In Lotto the expected value of the jackpot when the prize has present value P is*

$$\frac{P}{m\nu}(1-e^{-\nu}) \quad \textit{per ticket,} \tag{5}$$

where

$$m = \binom{\mu}{6}$$

and $n = m\nu$ is the number of tickets sold.

Proof: Another way of looking at eqn. (5) is instructive. Each ticket sold must have the same expected value; there are n tickets sold. The probability the prize will not be claimed is $e^{-\nu}$. Thus the expected gain g in dollars to the player for each ticket (tickets in *Lotto* are 2 per dollar) is

$$g = \frac{P\left(1-e^{-n/m}\right)}{n} - \frac{1}{2} \tag{6}$$

which is merely a rewriting of eqn. (5). ■

In order to obtain an idea of possible fluctuations in the player's expected gain for different values of the jackpot J which determine in some stochastic manner the relative participation, we make a few calculations for the Washington lottery.

Case 1: A prize of $J = \$3$ million attracted buyers of $n = 6.6 \times 10^6$ numbers. Since $\nu = 0.93$, with $m \doteq 7 \times 10^6$ we find from eqn. (3) the expected gain $g = -0.224$.

Case 2: $J = 2 \times 10^6$, with $n = 4.6 \times 10^6$, so that $\nu = .65$ and thus $g = -0.292$.

Case 3: $J = 5 \times 10^6$ produced $n = 8.7 \times 10^6$, thus $g = -0.093$.

Case 4: $J = 6 \times 10^6$, with $n = 13.1 \times 10^6$, hence $g = -0.114$.

It is not surprising that the expected gain is always negative but the relatively small fluctuation in the gain regardless of the size of the jackpot is not intuitive to most people. But we see that because of bigger prizes the consequent publicity and increased participation *does not allow the player's gain to increase significantly, if at all.* This is contrary to the usual expected value calculations done in Section II, and which seem to govern betting patterns.

Suppose that some knowledge of the distribution of ticket-sales is obtained, determined empirically as a function of the size of the proffered

jackpot. The distribution of participation could then be controlled through the proper choice of μ. (Recently Oregon has changed μ from 38 to 42). Thus, in a sense, the return to the state can be optimized by balancing the expected gain between the two alternatives of offering prizes that are large which return too much to the bettors, or offering prizes too small to elicit the volume of ticket sales necessary. Were the distribution of sales, as a function of jackpot size, known *a priori* this calculation of expected gain would be possible as well as the variance of the gain.

To illustrate this point we exhibit in Figure 2 a plot of the relationship between the nominal jackpot prize (usually paid in a 20-year annuity) and the consequent participation for 62 consecutive weeks in the Washington State Lottery. Note that if the present value of the prize were plotted, instead of the nominal value, the ordinate of each point would be reduced by about one-half, depending upon interest rates at the time the prize was awarded. This latter way is how the state regards the relationship between prize and participation.

The utility of the nominal prize may be different for each bettor, depending upon age or taxable income, and could change depending upon the size of the prize. In general the utility function seems to be convex for most people, who prefer to wager one dollar at astronomical odds in the hope of winning a million dollars rather than wager one dollar at the corresponding odds

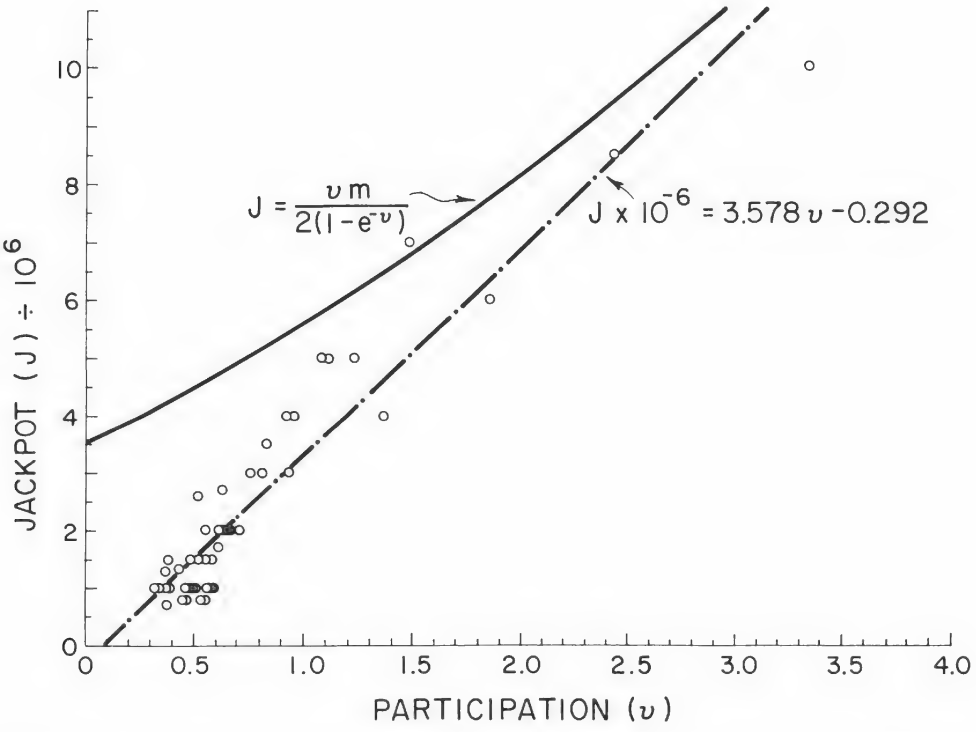

Figure 2. The scattered circles (o) plot the jackpot (in millions) versus relative participation for the first 61 weeks of the Washington *Lotto*. The solid curve is a plot of the function $2J = \nu m(1 - e^{-\nu})^{-1}$, the relationship between the jackpot and the relative participation which would give zero for the expected nominal gain ($g = 0$). For one week only, the expected gain to the player was positive (the single point above the curve); for this week it "made sense" to play the game. The line plots the linear regression of P on ν.

in order to win a thousand dollars. This was clearly the case in the New York state lottery, when a $41 million prize caused a "feeding frenzy" of participation by effecting sales of 80 million tickets in New York and surrounding states.

Discussion

As with many stochastic phenomena, the behavior of the various lottery games is often counter-intuitive. However, the observed "patterns" to these games are in fact consistent with the simplest null model of independent and equally-likely outcomes. For example, our analysis of the "pick-6" lottery games reveals that the weekly pattern of winning (*i.e.* no winner, one winner, multiple winners), though somewhat surprising, is easily explained. The empirical pattern of coincidences of lottery numbers in successive weeks, proposed by some observers as a useful "strategic" device in forming one's lottery selections, is also in accord with our (purely random) model of the lottery. The occurrences of "clusters" or "runs" is a salient feature of random processes, and their presence should not be misconstrued as offering a means to divine the future. This misconception seems to lie behind the most common schemes for advancing the prospects of lottery players. However, we state categorically that which we all know in our minds to be true: None of the various empirical (or metaphysical) systems for choosing lottery numbers will improve a player's chances of winning in a fair lottery. This sage advice is consonant with that presented by Packel (1981) and Adler (1985), which have not been "best sellers." This is in marked contrast to the evangelistic fervor of Howard (1984, 1985a,b) for the persistence of winning numbers, whose publications sell very well.

We conclude with the remark of a legislator of an earlier day that "lotteries are a tax on fools" and the sage advice "the only sure way to double one's money is to fold it once and put it back in one's pocket."

Literature Cited

Adler, W. 1985. *The Lottery Book.* Quill/William Morrow, Fairfield, New Jersey.

Feller, W. 1968. An *Introduction to Probability Theory and Its Applications.* Third Edition. John Wiley, New York.

Howard, G. 1984 State lotteries: how to get in it. *Gambling Times.* Issue 12, p. 78.

Howard, G. 1985a. How to handicap the Lotto numbers. *Gambling Times.* Issue 2, p. 78.

Howard, G. 1985b. Handicapping the Lotto numbers—Part II. *Gambling Times.* Issue 3, p. 78.

Mises, R. V. 1939. Über Aufteilungs- und Besetzungswahrscheinlichkeiten. Revue de la Faculté des Sciences de l'Université d'Istanbul, N.S., 4:313-334.

Packel, E. 1981. *The Mathematics of Games and Gambling.* The Mathematical Association of America. Mathematical Association of America, Washington, D.C.

Received 29 January 1987
Accepted for publication 26 May 1987

Roland C. Kufeld, Colorado Division of Wildlife
317 W. Prospect, Fort Collins, Colorado 80526

David C. Bowden, Department of Statistics
Colorado State University, Fort Collins, Colorado 80523

and

John M. Siperek, Jr., California Department of Fish and Game
601 Locust, Redding, California 96001

Evaluation of a Telemetry System for Measuring Habitat Usage in Mountainous Terrain

Abstract

Telemetry, the use of radio-transmitters to follow wildlife, has enjoyed popularity and widespread use because it can generate much animal location and activity data in a limited time. When animal locations are estimated by triangulation based on angle of signals received, rather than on visual contact, it becomes important to understand equipment limitations that may influence the accuracy of signal origin estimation. Problems of estimating signal origin are magnified in mountainous terrain by signal reflection. We tested directional accuracy of a precision-null antenna system in mountainous terrain of northcentral Colorado. Statistical tolerance limits applied to a two-wavelength system with two, three-element antennas, separated by two wavelengths, gave measurement error of no more than $\pm$ 3.4° (at least 90 percent of the time) at the 90 percent confidence level based on a mean of four readings per transmitting site, taken in rapid succession. A precision-null antenna system was found superior to a one-wavelength antenna type. Signal quality and accuracy in determination of signal directionality decreased with increased height of terrain obstacles between transmitter and receiver. Transmitter-receiver distance up to 4.6 km (the maximum tested) accounted for only eight percent of the variation in directional accuracy. Signal quality categories are described which can assist an operator in judging relative directional accuracy of received telemetry signals. A new approach to determining habitat usage by instrumented animals is described which utilizes percent composition of each vegetation type occurring in error polygons to reflect probability that the transmitter is located within a given vegetation type.

Introduction

Radio-telemetry is commonly used to locate animals when estimating home range size, daily movements, and habitat use (Tester and Siniff 1965, Craighead and Craighead 1973, Lindzey and Meslow 1977, and Irwin and Peek 1983). Few telemetry studies, however, have addressed limitations of the tracking systems being employed. The value of reported results would be enhanced if an analysis of the systems' limitations was included.

Heezen and Tester (1967) discussed influences on accuracy incurred in radio-telemetry triangulation and described an error polygon that delineates the bounds of a particular location within which an instrumented animal will be found. Error polygon boundaries determined by the intersection of error confidence limits or error arcs are discussed by Springer (1979). If each error arc has a confidence level of $1-\alpha$ of containing the true bearing of the transmitter, then the transmitter will be within the resulting error polygon formed from the two independent error arcs with confidence $(1-\alpha)^2$. In lieu of an error polygon, Hornbeck (1979) used a circle to represent the area of animal location. Circle size was based on a linear regression of location error and triangulation distance developed during preliminary experiments with a "test" transmitter. Rongstad and Tester (1969) used a grid system of 2.6 ha squares covering their study area and assumed the square from which a signal was received to be the location of their instrumented deer.

Accuracy of location decreases as error polygon size increases (Heezen and Tester 1967) so it is essential to use telemetry equipment that can detect signal directionality with a high degree of accuracy when triangulating. To be meaningful, error polygon size must be as small as possible. Heet (1977) reported an average error of 0.14 ha using triangulation for deer in Ohio. Springer (1979) also examined sources of bias in radio-telemetry and found no significant biases for observers, days, receivers, transmitters, and distance between transmitters and receivers when his "loudest signal method" was used.

Problems with accuracy are encountered in mountainous terrain as obstructions may block the most direct route of a signal from transmitter to receiver and cause the signal to be received from the direction of its path of least resistance through the terrain. Such distorted or "bounce" signals can result in directional accuracy error of many degrees (Hupp and Ratti 1983, Lee *et al.* 1985).

Springer (1979) has recommended that "future studies in which radiotelemetry is employed should devote some pilot effort to identify the factors that might affect bias and sampling error. The researchers should test these factors and determine the magnitude of the bias and sampling error, and then design an experiment with these results in mind." The purpose of this study was to determine directional accuracy of a precision-null antenna system in mountainous terrain and to facilitate a new approach to use of error polygons in a subsequent mule deer habitat usage study. Several modifications of an antenna system described by Hallberg *et al.* (1974), combined with certain antenna design characteristics used by Cochran *et al.* (1965) were tested in mountainous terrain near Red Bluff, California, by John Siperek. Two of the most accurate modifications were selected and subsequently compared in mountainous terrain near Fort Collins, Colorado, where the more promising modification was tested extensively.

Study Area

The study area is approximately five km west of Fort Collins, Larimer County, Colorado, and encompasses about 23 km2, including the east side of Horsetooth Mountain. It is bounded on the east by Horsetooth Reservoir, the west by the crest of Horsetooth Mountain, the south by County Road 38E, and the north by Empire Gulch. Elevation ranges from 1646 m at the reservoir shoreline to 2211 m at the highest point on Horsetooth Mountain. The area is characterized by rugged mountainous terrain with numerous rock outcrops, ridges and canyons. Vegetation types include ponderosa pine (*Pinus ponderosa*) with various canopy densities and interspersed with Douglas fir (*Pseudotsuga menziesii*); mountain shrubs consisting primarily of mountain mahogany (Cercocarpus montanus); wet meadow; grassland; and a riparian type with cottonwood (*Populus sargentii*), chokecherry (*Prunus virginiana*), wild plum (*Prunus americana*), skunkbush (*Rhus trilobata*), and hawthorn (*Crataegus erythropoda*).

Methods

Antenna System

The precision-null system consisted of two, vertically oriented, three-element, yagi antennas mounted parallel to each other (Figure 1). Antennas were wired 180° out of phase and connected at the mast by a union box or peak combiner. The system was designed for 149 MHz. The mast section inside the pickup camper, on which the system was mounted, was equipped with a compass rose and pointer for determining antenna direction. The system incorporated a telescoping mast and antennas that folded inward, making it easily portable by vehicle. A detailed description of the antenna system is available from the authors upon request. Adherence to construction details is critical to performance.

Figure 1. Precision null antenna system mounted on a pickup camper.

Antenna attitude was positioned, initially, each time it was used by orienting on a fixed beacon transmitter on Horsetooth Mountain with a known bearing from the receiver point and setting the compass rose pointer accordingly. When rotated 180°, this antenna received a signal in a pattern of four peaks and three nulls, which is apparent by listening to the signal while viewing the compass rose (Figure 2). The antenna was oriented toward the transmitter when receiving the center null. This null is from less than a degree to five or six degrees wide, depending on signal quality. A peak, another narrow null, and

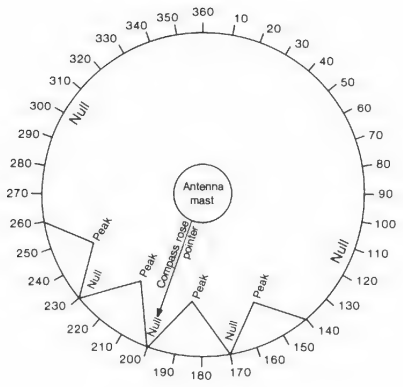

Figure 2. Signal pattern of peaks and nulls one would expect from a good quality signal using a two-wavelength antenna system. The compass rose pointer is oriented toward the center null, indicating direction to the transmitter is 200°.

another peak occur spaced about 15° intervals on each side of the center null. Nulls of about 90° in width occur beyond this outer peak. A similar pattern occurs on the rear side of the antenna, but peaks and nulls are poorly defined.

Signal direction is best established by determining two direction bearings with identical signal strength, each one a few degrees to the right and left of the null, and then by computing their mean to pinpoint the null centerpoint. This is recorded to the nearest 0.5°. Signals were classified as follows:

Signal Class 1. Loud and clear with little or no background noise. Patterns obvious and easy to read. Good symmetrical patterns with four peaks and three nulls. Peaks about 30° apart and nulls about 30° apart. Difference between peaks and nulls is readily discernable. Narrow center null (approximately 1° to 3°).

Signal Class 2. Loud but *with background noise.* Same as Signal Class 1 except center null may be larger and it may be necessary to bracket it by listening to the increasing signal levels 3° or 4° either side of it. However, it is still relatively easy to determine the null centerpoint.

Signal Class 3. Weak signal with much background noise. Pattern difficult to discern and difficult to read. Requires much time to establish the pattern. Relative difference between peaks and nulls is small. Peaks may not be symmetrical in intensity and peaks and nulls may be more or less than 30° apart. Nulls are wide and it is difficult to determine the null centerpoint.

Signal Class 4. No signal or signal too weak to establish any pattern.

Signal Class 5. Signals with two, four or more nulls regardless of signal strength.

Sampling Procedures

Several potential receiver points were selected near the study area perimeter to test signal directional accuracy. Efforts were made to select receiver points that offered maximum, unobstructed visibility of the area, and were free as possible of nearby terrain features that could cause incoming signal distortion. Some were found unsuitable during subsequent testing. Seven receiver points were retained. These were located on a ridge on the east and south sides of Horsetooth Reservoir.

Transmitting sites were located using a 1-ha grid system that encompassed the entire study area. A total of 111, 1-ha cells were randomly selected, and the center of each chosen cell became a transmitting site. The signal from each site was received from each of two different receiver points.

One observer located transmitting sites in the field through use of high quality 1:15840 scale, color aerial photos on which transmitting sites were plotted, and which were cut into photo quadrats small enough to be easily carried while the other operated the receiver. Both observers had previous telemetry experience and extensive experience using aerial photos to locate exact spots on the ground. Observers communicated by hand-held, two-way radios. Transmitters used for testing were 149 MHz radio-collars made for mule deer (*Odocoileus hemionus*). Transmitters and receivers were manufactured by Telonics, Inc.[1] (Mesa, Arizona). A transmitter was hung from a bush or limb 0.3 m to 1.0 m above ground at each of four locations within a 1.5-m radius of each transmitting site. The transmitter was

[1]Reference to this company does not imply endorsement by the State of Colorado.

moved among locations and a reading was taken at each location. The recorded bearing was a mean of the four readings from the site. The receiver operator did not know the direction to the transmitter placer. The compass bearing for each transmitting site was compared with the true transmitting site-receiver angle as measured on a large sized 1:14049 scale, high resolution, color infrared aerial photo taken by NASA from a U-2 plane at an altitude of 21,336 m. Distances and angles on this photo were compared with surveyed distances and angles on the ground. There was no apparent photo distortion.

In practice an estimate of an animal's location is made at a specific point in time. Consequently, a multitude of locations will be considered over the duration of a study involving many points in time and different animals. Hence, accuracy of individual location estimates is of concern, as contrasted to accuracy of the mean of many estimates involving different times and locations. Tolerance limits (confidence level $1-\alpha$ and proportion of population contained within the interval P) permit the statement that one can be 90 percent ($1-\alpha=0.9$) confident, using the same equipment and procedures, and under existing terrain conditions, that at least 90 percent ($P=0.9$) of the individual estimated locations will be within the calculated number of degrees of the actual transmitting site. Thus, in addition to calculation of sample mean bias and a corresponding confidence interval for true mean bias, tolerance intervals for the error of individual estimated locations were constructed as $\bar{x} \pm ks$ with $1-\alpha=.9$, $P=.9$ and $P=.75$. Dixon and Massey (1969, Table A-16) give k for selected values of n, $1-\alpha$ and P (Their γ is our $1-\alpha$). Degrees of error in location estimates were assumed to be normally distributed.

Preliminary directional accuracy comparisons of antenna systems constructed with one and two wavelength separation (2.00 m and 4.01 m, respectively) between antennas were made on the study area using 11 transmitting sites. Transmitter-receiver distance was about 0.8 km. Procedures were as previously described except that only one receiver point was used. The two-wavelength antenna was found superior and was subsequently tested extensively using all 111 transmitting sites.

Since observers alternated between operating the receiver and placing the transmitter at randomly selected sites throughout the study area, a test involving three people was conducted to determine degree of directional bias between observers. One individual placed the transmitter at four locations at each of 20 sites (situated at 30.5-m intervals) in a basin area where it had been determined that each signal class would be represented. Some sites were line-of-sight to the receiver (located 0.8 km from the basin area) while others were behind a 7.6-m cliff. Procedures for this test were exactly the same as used for sampling directional bias on the study area, except that signals were received by both observers who conducted the directional bias tests.

The 111 randomly selected transmitting sites and receiver points used to sample them were plotted on a 1:24000 scale U.S.G.S. topographic map with 40-ft (12.2-m) contours. Transmitter-receiver distance and signal clearance or lack of clearance of the highest terrain feature that occurred between the receiver and transmitter were measured on the contour map. To determine signal clearance for line-of-sight signals, perpendicular distance between the sightline and top of the highest terrain feature (elevationally) that occurred between receiver and transmitter was recorded and assigned a plus (+). If the signal path was not line-of-sight, indicating the signal was obstructed by terrain, distance between top of the highest terrain feature and a straight line between receiver and transmitter, through the terrain obstacle, was recorded and assigned a minus (−). Directional bias within each signal class was then compared with transmitter-receiver distance and with signal obstruction or clearance. These data were analyzed by a one-way analysis of variance followed by Tukey pairwise comparisons of means adjusted for unequal sample size.

Results

The one- and two-wavelength antenna systems received signals of Class 1 or 2 from four and eight transmitting sites, respectively, of the 11 sites tested. Class 3 signals were received from seven and three sites, respectively. Mean directional bias of Class 1 and 2 signals received from 11 sites with the one-wavelength system differed significantly from zero ($\bar{x}=+5.1°$; $se=0.35°$; 90 percent confidence interval $=+4.27°$ to $+5.92°$). Mean directional bias of Class 1 and

2 signals received from the same 11 sites with the two-wavelength system, however, did not differ significantly from zero ($x = +0.4°$; $se = 0.24°$; 90 percent confidence interval $= -0.50°$ to $+0.85°$) and variation in directional accuracy was lower. The two-wavelength system also gave a more discernible pattern of peaks and nulls.

Differences between observers in determining telemetry signal direction for individual and combined signal classes with the two-wavelength system were not significant ($P > 0.1$). There was 95 percent agreement by observers on classification of signals among the 20 locations. This suggests signal classes are well defined, and signals of each class can be readily recognized.

Mean directional bias with the two-wavelength system, based on 111 transmitting sites and readings from two receiver points per site, differed significantly from zero (Table 1) for Class 1 and 3, but not for Class 2 signals. Even though significantly different from zero, the highest possible bias at 90 percent confidence for Class 1 signals was only $+0.75$ degrees while it was -4.89 degrees for Class 3 signals. Tolerance limits on degrees of bias were much narrower for Class 1 and 2 signals than for those of Class 3 (Table 1).

Signal quality and accuracy in determination of signal directionality decreased with increased height of terrain obstacles between transmitter and receiver. Figure 3 shows that error in measuring transmitter-receiver directionality of all individual Class 1 signals (depicted by circles) is least among the three classes because they are clustered closest to $X = 0$ degrees, and that most Class 1 signals originated from a point above the top of the highest terrain object between the transmitter and receiver. A 95 percent confidence interval of mean clearance of the highest terrain feature between transmitter and receiver was 22 m ± 9 m. Thus, most Class 1 signals were unobstructed. Error in measuring transmitter-receiver directionality of individual Class 2 signals (depicted by squares in Figure 3) was greater than for Class 1 signals but less than for those of Class 3. Most Class 2 signals ($\bar{x} \pm t.025$ se) originated from a point below (5 m ± 10 m below) the top of the highest terrain object between the transmitter and receiver. Error was greatest in measuring individual Class 3 signals (depicted as diamonds in Figure 3) and the mean origin of Class 3 signals was 41 m ± 20 m below the top of the highest terrain object between transmitter and receiver. Figure 3 also shows that variation in measuring transmitter-receiver

TABLE 1. Directional accuracy ($\bar{x} \pm t$ 0.05 se) of signals received from randomly selected transmitting sites using a two-wavelength precision-null antenna system.

Signal class	No. of transmitting sites[1, 2]	Degrees of bias			Tolerance limits on degrees of bias at 90% confidence level[4]	
		$\bar{x}$	sd	90% conf.[3]	75% tol.	90% tol.
1	77	+0.5	1.89	+0.25 to +0.75*	± 1.7	± 2.4
2	71	+0.1	2.36	−0.37 to +0.57	± 3.1	± 4.4
1 and 2	148	+0.3	1.89	+0.04 to +0.56*	± 2.4	± 3.4
3	65	−2.9	9.59	−4.89 to −0.91*	±12.6	±18.0

[1]For each transmitting site the recorded bearing is a mean of four readings derived by placing the transmitter at four locations within a 1.5-m radius of the site.

[2]Each of 111 random transmitting sites was sampled from two receiver points. Thus, excluding Class 4 and 5 signals, signal directional accuracy is based on 213 mean readings.

[3]90 percent confidence interval for mean bias ($\bar{x} \pm t \setminus {}^{sd}/\sqrt{n}$).

[4]One can be 90 percent confident (using the same equipment and procedures, and under existing terrain conditions) that 75 or 90 percent of all signals of a particular class will be within a certain number of degrees of the actual transmitting site (Dixon and Massey, 1969:142).

*Denotes a significant difference from zero in directional bias at $\alpha = 10$ percent.

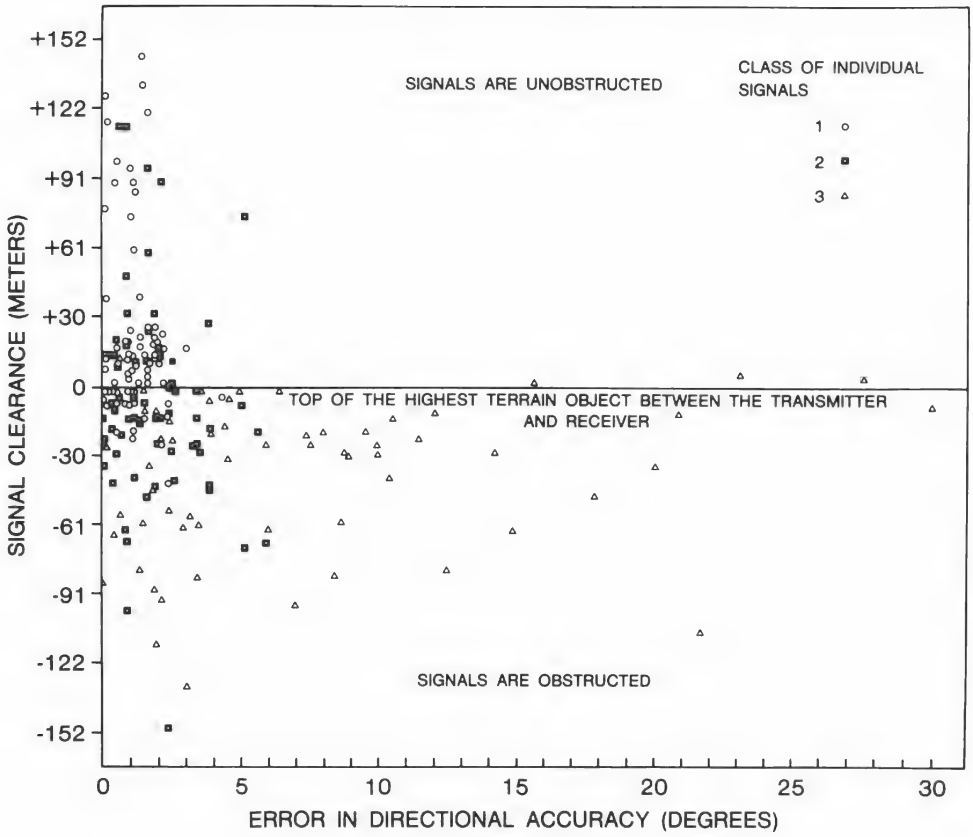

Figure 3. Distribution of Class 1, 2, and 3 signals showing degrees of error determination and origin of each individual signal with respect to the top of the highest intervening terrain object.

directionality of Class 1 signals was least, Class 2 signals second, and Class 3 signals greatest. Class 4 signals (N = 4) were transmitted from a mean of 122 m ± 53 m below the top of the highest terrain obstacle. The five class 5 signals received were emitted from a mean of 11 m ± 11 m below the top of the highest terrain obstacle. All pairwise differences among Class 1, 2, 3 and 4 signals in mean clearance or lack of clearance of the highest terrain feature existing between transmitter and receiver were significant ($P < 0.1$).

Our analysis of terrain effect by measuring only one feature, clearance height, is crude; it is reasonable to assume signal quality and directionality may have been even more closely related to terrain had it been possible to measure effects of all encountered terrain combinations on signal directionality.

Distance between transmitter and receiver up to 4.6 km, the maximum tested, did not appear to be an important factor influencing signal quality or directionality. There was poor correlation ($r = 0.280$—but more than zero correlation $P < 0.1$) between distance and directional accuracy of Class 1, 2, and 3 signals combined, and distance accounted for only eight percent of the variation in directional accuracy. Although mean distance between receiver and transmitter tended to be highest for Class 3 signals and lowest for Class 1 signals, there was a great deal of overlap in transmitter-receiver distances among the

three signal classes. Thus, accurate determination of signal directionality depended on whether the signal was obstructed by terrain and height of obstruction, regardless of distance.

Discussion

Lee *et al.* (1985) reported better precision ($P=0.02$, $N=10$) with nonmodulating signals from stationary transmitters than with modulating signals associated with transmitter movement. Our use of a mean of four location bearings within a 1.5-m radius of each transmitting site was an attempt to avoid trying to locate modulating signals, yet acquiring a mean directional bearing in the event a transmitter was attached to a slowly moving animal that stopped frequently as during feeding. In such an event, each of the four bearings would be taken only when the animal was momentarily still.

Hupp and Ratti (1983) reported good accuracy in relatively flat, open areas but found a large amount of error in directional accuracy associated with mountainous terrain. Lee *et al.* (1985) also reported a large amount of directional accuracy error in mountains. They used precision-null antenna systems with approximately one-wavelength separation. Hallberg *et al.* (1974) were able to use only one-half wavelength separation because their study area was flat. We found directional accuracy of the two-wavelength antenna system superior to the one-wavelength type in rugged terrain. Our sample of random transmitter locations covered a wide range of mountain terrain configurations and vegetation complexes.

Widths of tolerance intervals for Class 1 and 2 signals were considered sufficiently narrow to allow individual animal locations to be estimated with a reasonable level of accuracy (Table 1, Figure 3). The large standard deviation and, hence, wide tolerance limits for Class 3 signals (Table 1, Figure 3), however, were considered unacceptable. Thus, it is recommended that telemetry locations of radio-collared animals be based on Class 1 and 2 signals and that the receiver points be located to eliminate the occurrence of Class 3, 4, and 5 signals. The finding that a fairly large portion of signals (32 percent in this study) were classified as 3 and 5 and, thus, considered too inaccurate for use is unfortunate. However, it is better to be able to recognize an inaccurate signal by quality characteristics and exclude it than to include both accurate and inaccurate signals in one's data.

Accepting only good quality signals could bias an estimate of habitat usage or home range size if poor signals were consistently received from one portion of a home range. During a subsequent habitat usage study on the same area involving 27 instrumented mule deer during three winters, using only Class 1 and 2 signals, we were able, through careful receiver point selection, to get at least one location on each deer during 98 percent of 168 scheduled, six-hour monitoring periods. Thus, we conclude that a two-wavelength precision-null system using the mean of four readings per transmitting site (taken in rapid succession when the signal is not modulating), which results almost entirely in Class 1 and 2 signals, will serve to reduce the magnitude of error in detecting directionality of a radio signal in mountainous terrain. This will produce smaller error polygons when triangulating. Receiver points should be situated on prominent sites where nothing in the vicinity can interfere with incoming signals.

As magnitude of location error increases in habitat usage studies, the proportion of correct determinations of habitat types containing the transmitter will decrease. White and Garrott (1986) provide information describing the decrease in power of tests of no preference in habitat usage with increasing error in location estimation. Large sample size increases are needed to compensate for relatively small increases in location error. Thus, we recommend that, before a habitat usage study is conducted, performance of the antenna system and receiver sites be evaluated to determine if study area terrain conditions are such that meaningful results can be obtained. Error data derived from the preliminary evaluation of the antenna system and receiver sites can then be used in the following alternative procedure for measuring habitat usage based on error polygons.

Suppose each estimated location point in a habitat study will be based on one pair of triangulation bearings. Then, an error arc given by tolerance limits with $1-\alpha$ and P derived from the error analysis will be attached to each member of all pairs of triangulation bearings according to its signal class. Thus, with $(1-\alpha)$ 100 percent confidence at least 100 P^2 percent of

all error polygons contain the corresponding actual transmitter location. Habitat usage, then, is based on percent composition of each vegetation type occurring in the error polygon. Power of tests of no preference in habitat usage based on error polygon vegetation composition data can be substantially higher than the power that results when only the habitat type containing the estimated location point is considered. We recommend use of error polygons developed from tolerance limits since, at the given confidence level $(1-\alpha)$, the probability of all actual locations being in their error polygons does not depend on the number of error polygons constructed in the habitat usage study.

The best of $1-\alpha$ and P is not clear. As P is increased for fixed α, the size of error polygons increases. Larger error polygons will, in general, contain more habitat types and not necessarily have improved power in tests of no preference. Note that use of the habitat type containing the estimated location point only is the same as using $P=0$ in tolerance limit construction. Errors associated with four readings taken in rapid succession may not be independent. Thus, in our error analysis the mean of four such readings is considered to produce one bearing and, hence, one error. The standard deviation of these errors for each signal class is used in the tolerance limits construction. Actual transmitter locations are required to find these errors. Thus, error analysis is required separately from actual animal monitoring when error polygons are to be part of a habitat usage study. Our results from a deer habitat selection study based on these concepts will be forthcoming.

Acknowledgments

The study was financed by Federal Aid in Fish and Wildlife Restoration, Colorado Project FW 26P. We thank T. Fowler and H. Geduldig for assistance with fieldwork, L. Lovett for assistance in manuscript preparation, R. Morris, C. Bergman, and B. Mayer of Colorado Division of Parks and Recreation for their cooperation in making the study area available. We also thank A. E. Anderson, D. L. Baker, G. D. Bear, L. H. Carpenter, and N. T. Hobbs for critically reviewing the manuscript.

Literature Cited

Cochran, W. W., D. W. Warner, J. R. Tester, and V. B. Kueckle. 1965. Automatic radio-tracking system for monitoring animal movements. BioScience 15:98-100.

Craighead, J. J., and F. C. Craighead, Jr. 1973. Home ranges and activity patterns of nonmigratory elk of the Madison Drainage herd as determined by biotelemetry. Wildl. Mono. No. 33.

Dixon, W. J., and F. J. Massey, Jr. 1969. Introduction to statistical analysis. McGraw-Hill, New York.

Hallberg, D. L., F. J. Janza, and G. R. Trapp. 1974. A Vehicle mounted directional antenna system for biotelemetry monitoring. Calif. Fish Game 60:172-177.

Heet, G. C. 1977. Habitat utilization of white-tailed deer in southeastern Ohio as determined by radiotelemetry. Ohio State University, Columbus. M.S. Thesis.

Heezen, K., and J. R. Tester. 1967. Evaluation of radiotracking by triangulation with special reference to deer movements. J. Wildl. Manage. 31:124-141.

Hornbeck, G. E. 1979. Winter distribution, seasonal movements and cover type relationships of elk in southwestern Manitoba. Colorado State University, Fort Collins. M.S. Thesis.

Received 19 June 1986
Accepted for publication 1 June 1987

Hupp, J. W., and J. T. Ratti. 1983. A test of radio telemetry triangulation accuracy in heterogenous environments. *In* D. G. Pincock (ed.) Proc. Intnl. Wildl. Biotelem. Conf. Halifax, Nova Scotia. Pp. 31-46.

Irwin, L. L., and J. M. Peek. 1983. Elk habitat use relative to forest succession in Idaho. J. Wildl. Manage. 47:664-671.

Lee, J. E., G. C. White, R. A. Garrott, R. M. Bartmann, and A. W. Alldredge. 1985. Accessing accuracy of a radiotelemetry system for estimating animal locations. J. Wildl. Manage. 49:658-663.

Lindzey, F. G., and E. C. Meslow. 1977. Home range and habitat use by black bears in southwestern Washington. J. Wildl. Manage. 41:413-425.

Rongstad, O. J., and J. R. Tester. 1969. Movements and habitat use of white-tailed deer in Minnesota. J. Wildl. Manage. 33:366-379.

Springer, J. T. 1979. Some sources of bias and sampling error in radio triangulation. J. Wildl. Manage. 43:926-935.

Tester, J. R., and D. B. Siniff. 1965. Aspects of animal movement and home range data obtained by telemetry. Trans. North Amer. Wildl. Conf. 30:379-392.

White, G. C., and R. A. Garrott. 1986. Effects of biotelemetry triangulation error on detecting habitat selection. J. Wildl. Manage. 50:509-513.

Judith B. Glad, Consulting Plant Ecologist
1400 N Holman, Portland, Oregon 97217

Richard Mishaga, CH_2M HILL, Inc.
2020 SW Fourth Avenue, Portland, Oregon 97201

and

Richard R. Halse, Botanical Consultant
4535 NW Beta Place #3, Corvallis, Oregon 97330

Habitat Characteristics of *Sidalcea nelsoniana* Piper (Malvaceae) at Walker Flat, Yamhill County, Oregon

Abstract

The habitat characteristics of Nelson's checkermallow (*Sidalcea nelsoniana* Piper), a species proposed for listing by the U.S. Fish and Wildlife Service as threatened or endangered, were studied at Walker Flat, the site of the plant's largest population in the northern Oregon Coast Range. A proposed water supply reservoir would flood the site, eliminating the population. It was therefore necessary to discover if the site was unique or was critical habitat for the species. We found that *S. nelsoniana* is not habitat specific, but occurred in a variety of plant communities—grass meadows, sedge marsh, and heterogeneous wetland and riparian communities. *S. nelsoniana* exhibited tolerance for disturbance and for a variety of soil conditions. Soil textures ranged from clay to loam and exhibited considerable chemical variation. The species was not found on those portions of the site where soils remained wet throughout the growing season. The tolerance of *S. nelsoniana* for a variety of habitats may account for previous inconsistent reports about habitat preferences.

Introduction

Nelson's checkermallow (*Sidalcea nelsoniana* Piper) has been reported as endemic to the Willamette Valley of Oregon by Hitchcock (1957) and Hitchcock and Cronquist (1961). Descriptions of its habitat have been inconsistent and occasionally contradictory (Hitchcock 1957, Hitchcock and Cronquist 1961, Peck 1961, Meinke 1982). In 1984, the species was found at Walker Flat in the Coast Range of western Yamhill County, Oregon, where the City of McMinnville Water and Light Department (MWLD) has proposed to build a water supply reservoir.

S. nelsoniana is listed as a Category 2 plant, those for which information is inadequate to determine if listing as threatened or endangered is appropriate. They are, however, treated as under petition for listing (Fish and Wildlife Service 1985). This paper reports on studies undertaken at Walker Flat in 1985 to document the population size of *S. nelsoniana* there and the physical and chemical characteristics of the habitats in which it occurred.

Methods and Materials

Aerial photographs of Walker Flat were examined and vegetation cover types were identified and mapped on a large-scale contour map of the area. Sixteen grids were established for the inventory of *S. nelsoniana* (Figure 1). Grids were laid out in 15 m by 15 m blocks along a central baseline. All of the open areas of the site were entirely within grids. Forested margins and dense tree stands were searched during the flowering season.

The grids were mapped block by block on 2 and 3 July 1985. Each 15 m by 15 m block was divided into 1 m^2 plots (225 plots per block), which were examined individually. This technique yielded frequency values for *S. nelsoniana* at each grid (Frequency = [number of plots in which *S. nelsoniana* occurred/total number of plots examined] $\times$ 100). The relative cover of *S. nelsoniana* was visually estimated at each grid after mapping was completed. Mapping data were summarized and frequency values were calculated for each grid.

Ten stations for collection of physical and chemical habitat conditions data (HC stations) were established on 12 April 1986 (Figure 1). Their locations were randomly determined. Labeled stakes were driven into the ground to mark each station.

The first habitat conditions measurements were taken on 12 April 1985, followed by

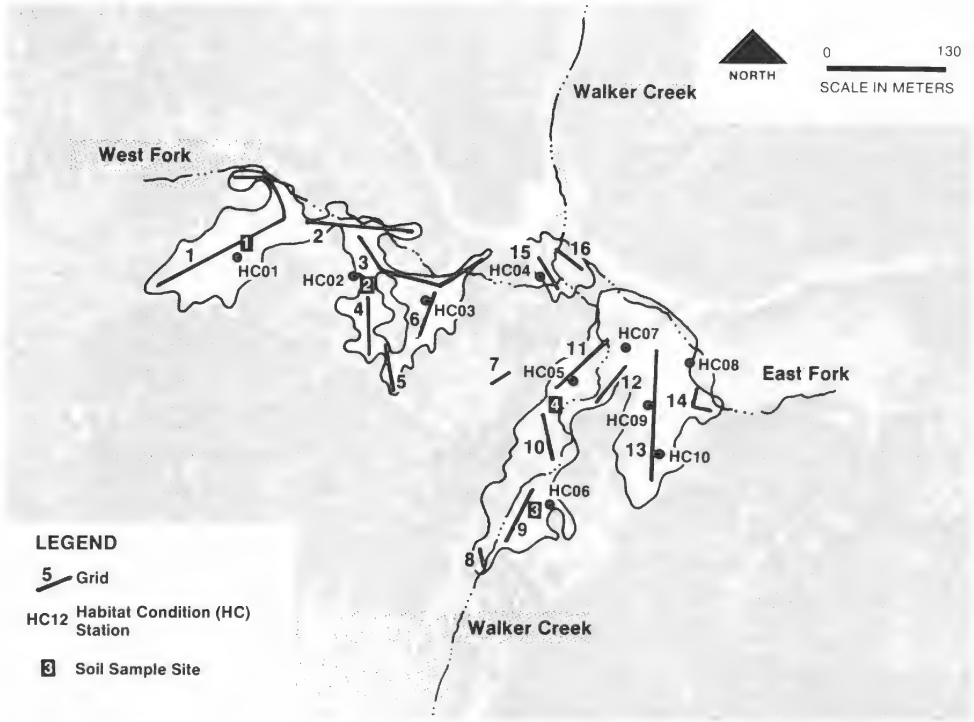

Figure 1. Approximate locations of mapping grids at Walker Flat.

sampling at monthly intervals through 19 March 1986. Air temperature, soil pH, soil temperature, and soil moisture were measured at each station. Since soil temperature, pH, and moisture measurements required disturbing the soil, each sample was taken at a different location within a 1 m radius of the stake.

Air temperature was measured by hanging a mercury thermometer on a shaded branch as near as possible to the stake marking the station. It was allowed to equilibrate for at least one minute before it was read to the nearest 0.5°C. Mean air temperatures for each sampling day were calculated. A recording thermometer was installed on 10 April 1985 at MWLD's weather station at McGuire Dam, about 1.1 km from Walker Flat and at approximately the same elevation. During data analysis, comparisons were made between temperatures at sampling stations and those at McGuire Dam for the same time period.

Precipitation records from McGuire Dam and from the National Weather Service station at Haskins Dam, located about 7.5 km from Walker Flat and at a lower elevation, were obtained to document precipitation patterns at Walker Flat.

Soil pH was measured on a sample taken from the bottom of a 10 cm deep, freshly dug, hole, using a pH Computer Acid/alkaline Soil Tester (Environmental Concepts). Soil temperatures were measured with a dial-type thermometer with a 30-cm stainless steel probe, scribed at 5 cm, 10 cm, and 20 cm from its tip. It was pushed into the soil to the 5 cm depth and allowed to equilibrate for about 1 minute, then a reading was taken to the nearest 0.5°C. This procedure was repeated at 10 cm and 20 cm, without removing the probe from the soil. Mean soil temperatures were calculated at each depth for each sampling day.

Soil moisture was measured with a "Quick Draw" Soilmoisture Probe (Soilmoisture Equip-

ment Company). The probe was inserted into a 20-cm deep hole made with the coring tool supplied with the instrument. After about one minute, during which the tip of the probe was allowed to reach approximately the same temperature as the soil, adjustments began and were continued until the reading (in centibars of soil suction [1 centibar = 1 kPascal]) became constant.

Soil texture and chemistry samples were taken at four sites on 13 August 1985. The sites were representative of the different habitats in which *S. nelsoniana* was relatively abundant. Samples 1, 2, and 3 were taken near stations HC01, HC02, and HC06, respectively. Sample 4 was taken about 50 m south of HC05. Soil from just beneath the surface to about 20 cm deep was mixed thoroughly. Plant material and stones were removed to the extent possible. Samples were analyzed by the Oregon State University (OSU) Soils Testing Laboratory and Soil Physics Laboratory.

Results and Discussion

Six vegetation cover types were identified and mapped (Figure 2): grass meadow, sedge marsh, heterogeneous wetland vegetation, riparian tree/shrub, forest, and disturbed area. The grass meadow, sedge marsh, riparian tree/shrub, and forest cover types included two or more distinct plant communities having sufficient similarity of species composition or community structure to be grouped together under a vegetation cover type map category.

The results of the *S. nelsoniana* mapping survey are presented in Table 1. Of the more than 37,000 1 m² plots examined at Walker Flat, 9.2 percent contained *S. nelsoniana.* The frequency of *S. nelsoniana* varied among the sixteen grids from zero to over 22 percent. Its cover never

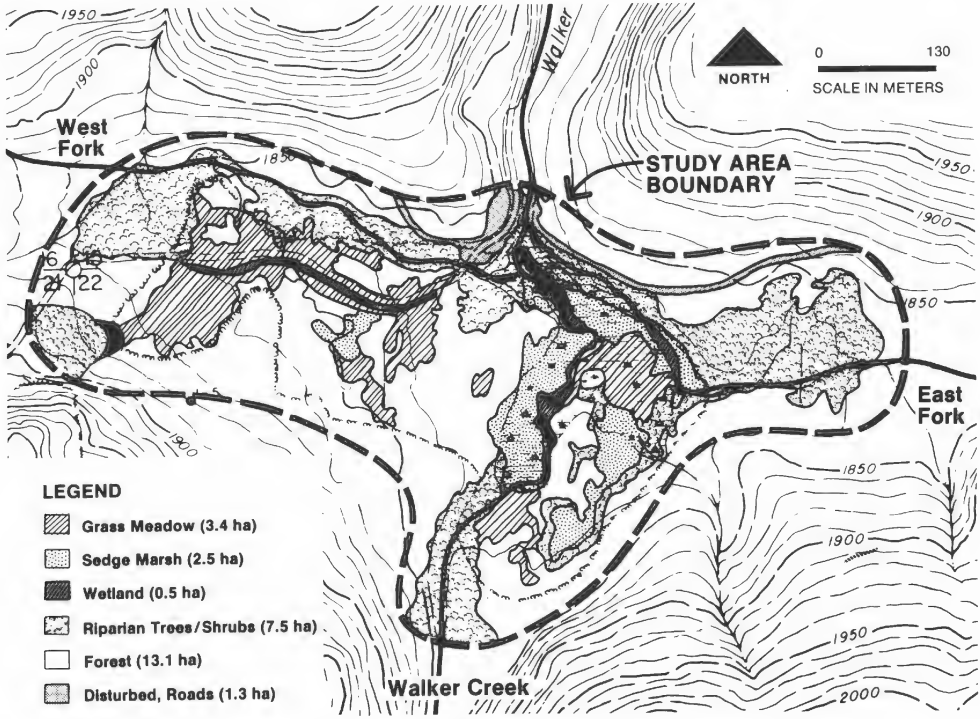

Figure 2. Vegetation cover types at Walker Flat.

TABLE 1. Summary of *Sidalcea nelsoniana* grid mapping data from Walker Flat, 1985.

Grid No.	Vegetation Cover Type[1]	Approximate Area (ha)	Total Plots[2] On Grid	Percent Frequency[3] Per Grid	Percent Cover[4] Per Grid
01	GM, SM, WA	0.88	9002	22.21	<3
02	GM, WA	0.20	2025	15.41	<2
03	GM, WA	0.25	2476	10.42	<1
04	SM, WA	0.13	1351	5.70	<2
05	GM	0.09	899	0.89	<1
06	GM, SM	0.25	2474	7.60	<1
07	GM	0.02	225	0.89	<1
08	RI	0.05	500	0.00	0
09	GM, SM, RI	0.44	4391	5.47	<1
10	SM, GM	0.13	885	3.52	<1
11	SM, GM	0.27	2700	0.15	<1
12	WA	0.09	900	0.00	0
13	GM, SM, WA	0.58	5864	1.62	<1
14	SM, GM	0.05	450	1.11	<1
15	SM, GM	0.09	909	0.11	<1
16	GM	0.05	449	3.56	<1
TOTALS		3.57	35502		

[1]The first vegetation cover type listed covered most of the grid; the rest were also present. GM = grass meadow, SM = sedge marsh, WA = heterogeneous wetland vegetation, RI = riparian trees/shrubs.

[2]Plots were 1 m^2.

[3]Percent frequency $= \frac{\text{number of 1 } m^2 \text{ plots containing } \textit{Sidalcea nelsoniana}}{\text{total number of 1 } m^2 \text{ plots in grid}} \times 100$

[4]Percent cover $= \frac{\text{area of grid covered by } \textit{Sidalcea nelsoniana}}{\text{total area of grid}} \times 100$

exceeded 3 percent and was usually less than 1 percent. The distribution of *S. nelsoniana* varied considerably among vegetation cover types and plant communities. Vegetation cover types and their constituent plant communities are discussed below, together with qualitative estimates of the abundance of *S. nelsoniana* within each plant community.

Grass Meadow. S. nelsoniana occurred in all the grids that included grass meadows and reached its greatest abundance in the west grass meadow area (grids 01, 02, and 03). These communities remained relatively dry throughout the year. Most of the grasses were introduced species (e.g., meadow fescue [*Festuca pratensis* Huds.], tall fescue [*Festuca arundinacea* Schreb.], velvetgrass [*Holcus lanatus* L.], orchard-grass [*Dactylis glomerata* L.]) and occurred only in the grass meadows. Such forbs as night-blooming morning-glory (*Convovulus nyctagineus* Greene), Oregon iris (*Iris tenax* Dougl.), early blue violet (*Viola adunca* Sm.), and buttercups (*Ranunculus* spp.) were present, but their abundance did not approach that of grasses. Shrubs (e.g., serviceberry [*Amelanchier alnifolia* Nutt.], common snowberry [*Symphoricarpos albus* (L.) Blake], and clustered wild rose [*Rosa pisocarpa* Gray]) were usually

scattered throughout the meadows. Most of the areas mapped as grass meadows contained low pockets supporting dense stands of slough sedge (*Carex obnupta* Bailey). Other *Carex* species were thinly scattered among the grasses and forbs.

Sedge Marsh. The five sedge marsh communities at Walker Flat were found on soils that ranged from flooded to moderately dry.

A commonly occurring wet sedge marsh community covered large portions of grids 10 and 11, areas where *S. nelsoniana* was never found. Dominated by small-fruited bulrush (*Scirpus microcarpus* Presl.) and creeping buttercup (*Ranunculus repens* L.), this community occurred on the lower floodplain of Walker Creek and its tributaries. The soil remained noticeably wet throughout the summer.

S. nelsoniana was not found in the wet sedge marsh community where bigleaf sedge (*Carex amplifolia* Boott) and marsh violet (*Viola palustris* L.) were among the dominants. This community occurred along the main stem of Walker Creek and in the triangle formed by the confluence of the main stem and the east fork. Standing or running water was present throughout most of the summer. Most of grid 15 was in this plant community.

S. nelsoniana occasionally occurred in the drier sedge marsh community dominated by *C. obnupta* and California false hellebore (*Veratrum californicum* Durand var. *caudatum* [Heller] Hitchc.). This community was primarily at the upper ends of grass meadows (e.g., Grids 01 and 13), where drainage from adjacent uplands apparently occurred as sheet flow following precipitation.

S. nelsoniana was fairly common in the driest of the sedge marsh communities where *C. obnupta,* bigleaf lupine (*Lupinus polyphyllus* Lindl. var. *polyphyllus*) and Douglas' aster (*Aster subspicatus* Nees) dominated. This community was most extensive at Grid 04. Standing water was present in low pockets during April and early May, but the soil dried as the season advanced. The wet soil appeared to be due partly to poor drainage and slow percolation and partly to high seasonal water tables.

S. nelsoniana often occurred in the ecotone between pockets of *C. obnupta* in low areas and the surrounding grass meadow. This sedge marsh community was dry throughout the summer.

Heterogeneous Wetland Vegetation. S. nelsoniana was found only where the soil dried in early summer in this cover type. No consistent community composition or structure was apparent. This cover type usually occurred along ditches or drainage channels or near the creeks where water backed up behind inactive beaver dams.

Riparian Trees/Shrubs. S. nelsoniana was rarely found in areas mapped as Riparian Trees/Shrubs along Walker Creek and its tributaries.

Three distinct riparian communities occurred at Walker Flat. They formed a transition zone between wetland and upland and included elements of each, as described by Oakley *et al.* (1985). A red alder (*Alnus rubra* Bong) community on the main stem of Walker Creek is the terminus of a riparian forest that lines the banks of Walker Creek for some distance upstream. Vine maple (*Acer circinatum* Pursh) was a major component of the shrub stratum, and the herb stratum supported an abundant growth of mesic forbs. The riparian zone along the west fork of Walker Creek supported an *Alnus rubra*-conifer overstory with skunk cabbage (*Lysichitum americanum* Hulten & St. John), abundant mosses, and few large but scattered shrubs. Crown closure was nearly complete, with very little light reaching the understory. *A. rubra* and willow (*Salix* spp.), with various accompanying shrubs and a variety of understory species, grew sporadically along the banks of Walker Creek and its tributaries. Douglas' spiraea (*Spiraea douglasii* Hook.) also grew in small but dense stands near the north end of Walker Flat and scattered along the east fork.

Forest. S. nelsoniana occurred only at the edges of forest communities where sunlight reaches the ground for more than half the day. Most of the forest map units comprised second-growth conifer communities dominated by Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco). Salal (*Gaultheria shallon* Pursh) was the most frequent understory dominant, with swordfern (*Polystichum munitum* [Kaulf.] Presl), and Oregongrape (*Berberis nervosa* Pursh) occasionally achieving dominance. Seedling and sapling western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) and grand fir (*Abies grandis* [Dougl.] Forbes) were common.

A few small, mixed conifer-hardwood stands occurred on the edges of the open areas. Western crabapple (*Pyrus fusca* Raf.) and black hawthorn (*Crataegus douglasii* Lindl.) were frequently seen in the bottomlands on the southwest side. The mixed forest communities were extremely variable as to understory species.

Disturbed Areas. The disturbed area mapped at the north end of Walker Flat is a graded parking area beside a road. It also served as a camp site, as evidenced by the presence of a fire ring and depositions of garbage and trash. It supported a thin growth of mostly weedy herbs. A few *S. nelsoniana* occurred at the edge of the parking area near the fire ring where disturbance was evident. This map category also included a gravel pit north of Walker Flat and the roads within the study area.

S. nelsoniana occurred at or near 5 of the 10 habitat conditions stations (HC01, HC02, HC03, HC06, and HC09). The other five stations were in plant communities where *S. nelsoniana* was never found or where it occurred only in the ecotones between them and adjacent upland communities.

Air temperatures at Walker Flat were higher than those recorded at McGuire Dam for the same time period. No correlation was made between air temperatures and other measured environmental parameters. Measured air temperatures at Walker Flat did, however, fall within the monthly ranges recorded at McGuire Dam.

Individual habitat conditions stations showed some variations in soil temperatures but all followed the same trends at each measured depth. Mean temperatures at all depths were calculated. Soil temperatures were highest on 22 July 1985 (20°C at 5 cm, 17°C at 10 cm, 15.5°C at 20 cm) and lowest on 18 December 1985 (−2°C at 5 cm and 10 cm, −3.5°C at 20 cm).

Soil pH values varied somewhat at each station over the period of sampling. All stations had mean field pH values in the range 6.5 to 7.0.

Soils remained wet at three stations (HC04, HC05, and HC08) throughout the sampling period. At all other stations, soils were wet to moist (5 to 25 centibars of soil suction) in spring 1985, then dried (25 centibars and higher) as summer advanced. Soil moisture increased again through fall and winter, but reached saturation (0 centibars) only at stations HC04, HC05, and HC08. Five of the stations were within 2 meters of *S. nelsoniana* plants (HC01, HC02, HC03, HC06, and HC09). The speices was never found near the three stations where soils remained wet (HC04, HC05, and HC08). The results of soil moisture sampling indicate that *S. nelsoniana* is intolerant of permanently wet soil.

A comparison of Haskins Dam normal (1968-1983) precipitation with precipitation recorded at McGuire Dam showed that, while fall precipitation (October through December) was somewhat greater than normal, rainfall during winter and spring 1985 was nearly 40 cm short of normal. This variation may have resulted in drier than normal soils at Walker Flat during the 1985 growing season; however, the dominance of upland grass species in the grass meadow communities indicates that those areas always dry out during the summer. Runoff and seepage from adjacent slopes also may have contributed to soil moisture, but most of it was apparently restricted to drainage channels through the grass meadows.

Laboratory pH values were substantially lower than those measured in the field. Daubenmire (1974) noted that field tests for pH often give higher readings than do laboratory tests because of CO_2 in the soil that dissipates during sample handling. Although all four soil sample sites supported *S. nelsoniana,* there were substantial differences in soil chemistry as well as in soil texture (Table 2). There were especially large variations in the major nutrients. A large variation in percent organic matter also indicated substantial differences in the soils. These differences indicate that *S. nelsoniana* tolerates a fairly wide range of soils conditions.

The *S. nelsoniana* at Walker Flat were vigorous, healthy plants. Signs of predation by both insects and larger herbivores were evident, but not to the extent that the apparent vigor of the growing plants was affected. Furthermore, despite an unusually dry winter and soils that dried out considerably through the summer months, *S. nelsoniana* did not seem to be affected by water stress.

S. nelsoniana is not habitat-specific. At Walker Flat it was found in all but the wettest areas and forests. It did extend a short distance into the ecotones between herb and adjacent forest communities, as long as tree canopy was sparse. It was found in all but one of the

TABLE 2. Chemical and physical characteristics of four soil samples collected at Walker Flat, 1985.

	Sample Number			
Chemical Analysis[1]	1	2	3	4
Laboratory pH	5.5	5.1	5.3	5.3
P (ppm)	9	5	3	2
K (ppm)	281	187	168	98
Ca (meq./100g)	14.5	12.1	15.2	15.2
Mg (meq./100g)	8.1	7.8	7.6	5.2
Na (meq./100g)	0.17	0.31	0.36	0.25
B (ppm)	0.39	0.42	0.37	0.36
Total N (%)	0.34	0.32	0.38	0.30
NH_4-N (ppm)	17.0	27.9	19.9	41.0
NO_3-N (ppm)	8.1	16.5	5.7	5.7
Organic matter (%)	6.01	14.97	9.38	19.12
Textural class[2]	Silty clay loam	Clay	Clay	Loam

[1]Results reported by OSU Soils Testing Laboratory.
[2]Results reported by OSU Soils Physics Laboratory.

vegetation cover types. It was also observed to have some tolerance for disturbance. During the summer the parking area north of Walker Flat supported a weedy flora that included *S. nelsoniana.* Motorcyclists damaged Grid 04 in late June, cutting deep tracks into the grid area and churning and damaging roots and rhizomes. Despite this, *S. nelsoniana* plants along the torn paths matured and produced flowers and fruits.

The apparent tolerance of *S. nelsoniana* to a variety of habitat conditions may account for the inconsistent habitat information that was previously reported.

Literature Cited

Daubenmire, R. 1974. Plants and Environment. John Wiley & Sons, New York.

Hitchcock, C. L. 1957. A study of the perennial species of *Sidalcea.* Univ. Wash., Publ. Biol. 18:1-79.

Hitchcock, C. L., and A. Cronquist. 1961. Flora of the Pacific Northwest, Part III. University of Washington Press, Seattle.

Received 22 April 1986
Accepted for publication 4 June 1987

Acknowledgements

This study was supported by the City of McMinnville, Water and Light Department, as part of a cooperative investigation with the U.S. Bureau of Land Management, Salem District, concerning the status and distribution of *Sidalcea nelsoniana.* The authors wish to express their thanks to LaRea Dennis of the Oregon State University Herbarium for her assistance in verifying the identification of *Sidalcea* specimens and to Vickie Nissen of CH_2M HILL, Inc. for preparation of the figures.

Meinke, R. J. 1982. Threatened and Endangered Vascular Plants of Oregon: An Illustrated Guide. U.S. Fish and Wildlife Service, Portland.

Oakley, A. L., J. A. Collins, L. B. Everson, D. A. Heller, J. C. Howerton, and R. E. Brown. 1985. Riparian zones and freshwater wetlands. *In* E. R. Brown (ed.) Part 1. Chapter Narratives: Management of Wildlife and Fish Habitats in Forests of Western Oregon and Washington. U.S. Forest Service, Portland.

Peck, M. E. 1961. A Manual of the Higher Plants of Oregon. Binford & Mort, Portland.

William R. Gould, Montana Cooperative Fishery Research Unit
Montana State University
Bozeman, Montana 59717

Features in the Early Development of Bull Trout (*Salvelinus confluentus*)

Abstract

The early development of bull trout through the absorption of the yolk sac was observed. Brain subdivisions, optic cups, auditory vesicles, somites, pectoral fin buds, olfactory pits, liver and opercular openings had appeared by 167 Celsius temperature units (CTU). Melanophores and blood had formed by 206 and 288 CTU, respectively. At 443 CTU newly hatched fish had rays in the median fins. A gular ridge appeared at 724 CTU and the yolk sac was absorbed at 810 CTU. The early development of bull trout largely paralleled those of other species of *Salvelinus* in North America. However, the development of bull trout differed from other members of the genus in the order of appearance of pectoral fin buds and melanophores in relation to other features, the fixed size of oil globules in the yolk sac, the degree of development of the vitelline vein complex during the embryonic stage and the presence of a gular ridge in larvae. The gular ridge is apparently diagnostic for bull trout larvae and provides a means of identifying the larvae of this species, which will permit the identification of spawning areas and evaluations of spawning success from ichthyoplankton samples.

Introduction

Five species of *Salvelinus* occur in North America (Robins *et al.* 1980). The early development of four of these, the lake trout (*Salvelinus namaycush*), Arctic char (*S. alpinus*), brook trout (*S. fontinalis*) (Balon 1980a, b, c) and Dolly Varden (*S. malma*) (Blackett 1968) has been described. This account presents the first report on the appearance of features in the early development of the remaining species, the bull trout (*S. confluentus*), a native of the northwestern United States and Canada (Cavender, 1978).

Methods

Fertilized eggs were obtained by mixing the eggs and sperm from one female and two male bull trout from Whale Creek, a tributary of the North Fork of the Flathead River, Montana, on October 12, 1984. The eggs were then water-hardened, transported to the Bozeman Fish Technology Center, and reared in an incubation tray.

After organogenesis, random samples were taken at 2-9 day intervals with most samples being collected at 7 day periods. Live specimens and material preserved in 10 percent formalin from each sample were examined in transmitted and reflected light under a 7-30X dissecting microscope. Some preserved specimens were also treated with hematoxylin and/or glycerine prior to examination. Specimens taken before hatching were termed embryos and those after hatching were called larvae (Lagler *et al.* 1977). The total lengths reported are for preserved fish.

Study specimens were held in an incubation tray with a flow-through circulation of spring water chilled in a Living Stream[1] Model BAL 1076 apparatus. Water temperatures in the incubation tray were recorded on a Foxboro Model 12R continuous temperature recorder. Celsius temperature units (CTU) were calculated from hourly temperatures on the thermograph charts following the procedure of Leitritz and Lewis (1976). Dissolved oxygen levels were measured periodically by the Winkler method during the incubation period.

Results

Bull trout embryos and larvae were raised under water temperatures that fluctuated from 4.5 - 8.0°C and dissolved oxygen levels of 7.5 - 8.0 mg/l. The time and order of appearance of features noted under this regime are presented in Table 1.

Sensory organs, muscle formation and brain differentiation appeared early in the developmental process and before melanophore formation. Circulatory and digestive system formation and

[1]Reference to trade names does not constitute U.S. Government endorsement of commercial products.

TABLE 1. The time and order of appearance of features in the early development of bull trout.

Day after fertilization	Cumulative Celsius temperature units (CTU)	Number of specimens examined	Average total length (mm)	Appearance of developmental features
5	38	10		Vitelline membrane, yolk sac and blastoderm averaged 5.4, 5.0 and 1.7 mm in diameter, respectively (Fig. 1).
26	167	8	5.7	Forebrain, midbrain and two areas of hindbrain formed (Fig. 2). Optic cups with lenses and auditory vesicle evident. Somites present in head and throughout body. Pectoral fin buds and liver forming. Olfactory pits and opercular openings apparent.
33	206	8	7.2	Eyes with a few melanophores. Pharyngeal arches and anus visible. Vitelline vessels on left side of yolk sac prominent.
40	245	8	8.4	Beating heart apparent. Liver distinct and eyes densely pigmented. Mouth open and vitelline vein formed weak loop on front of yolk sac.
47	288	9	9.8	Melanophores scattered on head but in bands on body (Fig. 3). Jaws forming and bile showing in hind gut. Blood obvious in dorsal aorta, post-cardinal vein, heart and blood islands on yolk sac. Vitelline loops on yolk sac not evident.
55	332	9	10.8	Melanophores on peritoneum. Blood moving through gill arches. Vitelline vein on left side of yolk sac well developed.
61	372	9	12.7	Trunk flexing. Jaws moving sporadically. Melanophores scattered between lateral and dorsal bands of melanophores. Dorsal fin being set off in dorsal finfold. Basal portion of anal fin rays faintly visible.
68	410	8	12.6	Opercular and pectoral fin movements. Opercular openings anterior to three gill arches and pelvic fins forming.
73	443	8	14.7	Some hatching. Caudal fin rays well defined. Basal portions of dorsal and anal fin rays present. Oil globules in yolk sac no larger than 0.25 mm in diameter.
75	456	9	15.3	Opercula cover gill arches. Melanophores present on upper jaw and on caudal fin.
82	503	9	16.6	Hatching nearly complete. Diffuse spot on caudal fin. Pectoral fin rays indistinct and anal fin being set off in finfold.
89	548	10	18.5	Distinct pectoral fin rays. Melanophores scattered along base of dorsal finfold, dorsal area of yolk sac and chin (Fig. 4). Opercula and mouth opening and closing regularly. Swimming observed.
94	586	10	19.7	Concentration of melanophores on body near base of caudal fin.
103	644	10	21.7	Notches in dorsal finfold identified location of future adipose fin. A few melanophores near adipose fin, around heart, on gill arches and fleshy bases of pectoral fins.
110	687	10	22.1	Pelvic fin rays poorly defined. A few melanophores present on pectoral fin membranes.
117	724	10	23.2	A median ridge prominent between the chin and isthmus (Fig. 5). Chromatophores present on anterior edge of dorsal fin.
124	767	9	23.8	Endogenous materials being excreted.
131	810	9	23.9	Finfold absent anterior to dorsal fin but present posteriorly. Ventral finfold persisted anterior and posterior to pelvic fins (Fig. 6). Yolk sac not apparent. First melanophores on belly appeared between pectoral fins. Pelvic and anal fins still without melanophores. Parr marks appearing.

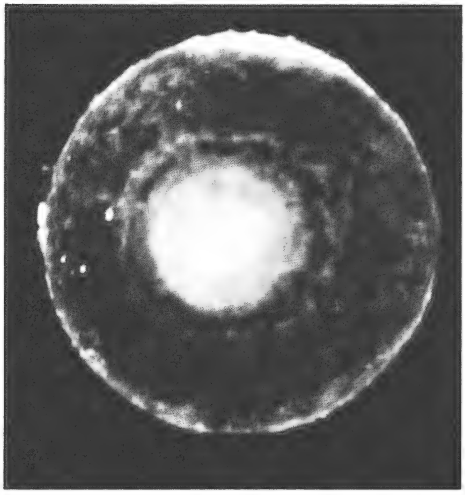

Figure 1. Embryo at 38 CTU with 1.7 mm diameter blastoderm.

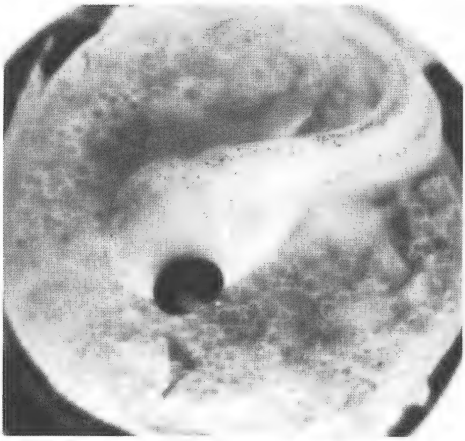

Figure 3. Embryo at 288 CTU with melanophores heavily concentrated in eyes, scattered on head and in bands on the body.

Figure 2. Embryo at 167 CTU showing brain, optic, auditory, pectoral fin bud and somite development.

Figure 4. Larva at 548 CTU showing dorsal and anal fin sites, gular ridge and caudal blotch.

Figure 5. Larva at 724 CTU with close up of gular ridge.

Figure 6. Larva at 810 CTU with only small portions of dorsal and anal fin folds remaining.

finfold differentiation largely occurred following melanophore appearance.

Discussion

The occurrence of specific events in the early development of bull trout and Dolly Varden cannot be readily compared to like events in the development of other North American *Salvelinus* on a temperature unit basis because these species were reared under fluctuating water temperatures. However, the order of appearance of structures in salmonids raised under less than extreme environmental conditions is relatively fixed (Ballard 1973). Therefore, the developmental patterns of salmonids can be compared and Balon (1980d) has done so for lake trout, Arctic char, brook trout and Dolly Varden.

Comparison of the pattern of early development of bull trout to those of other North American *Salvelinus* species indicates many similarities and a few differences. In bull trout, pectoral fin buds formed before melanophores, heart beats, blood and vitelline veins were seen. However, in lake trout the pectoral fin primordia formed after the latter three features had appeared. The oil globule in the yolk sac of bull trout did not increase in size at the end of cleavage as Balon (1980b) reported for Arctic char. The vitelline vein complex in bull trout developed strongly only on the left side of the yolk sac and not on the right side as reported for Arctic char (Balon 1980b) and brook trout (Balon 1980c). Melanophores appeared on the bodies of bull trout before fin rays developed, whereas, this order of appearance was reversed in Dolly Varden (Blackett 1968). These differences in the early development of bull trout and other named species of *Salvelinus* appear to be of the same magnitude as differences between other species of North American *Salvelinus* (Balon 1980d). However, the gular ridge noted in bull trout larvae apparently is unique and should allow the identification of the larvae of this species from those of other *Salvelinus* in larval fish samples. This will permit biologists to identify the spawning areas and evaluate the spawning success of bull trout.

Acknowledgements

I thank the Bozeman Fish Technology Center for providing facilities for the project. I am grateful to Thomas Weaver who supplied the bull trout eggs and measured dissolved oxygen levels. Darrel Snyder, Dr. Paul Eschmeyer and two unknown reviewers for this journal provided constructive criticism of the manuscript and Merrie Mendenhall photographed the bull trout specimens. Unit Cooperators are the U.S. Fish and Wildlife Service, Montana State University, and the Montana Department of Fish, Wildlife and Parks.

Literature Cited

Ballard, W. 1973. Normal embryonic stages for salmonid fishes, based on *Salmo gairdneri* Richardson and *Salvelinus fontinalis* (Mitchill). J. Exp. Zool. 184:7-26.

Balon, E. K. 1980a. Early ontogeny on the lake charr, *Salvelinus (Cristivomer) namaycush. In* E. K. Balon (ed.). Charrs: salmonid fishes of the genus *Salvelinus*. Dr. W. Junk Publishers, The Hague, The Netherlands. Pp. 485-562.

_____. 1980b. Early ontogeny on the North American landlocked arctic charr-sunapee, *Salvelinus (Salvelinus) alpinus oquassa. In* E. K. Balon (ed.). Charrs: salmonid fishes of the genus *Salvelinus*. Dr. W. Junk Publishers, The Hague, The Netherlands. Pp. 563-606.

_____. 1980c. Early ontogeny of the brook charr, *Salvelinus (Baione) fontinalis. In* E. K. Balon (ed.). Charrs: salmonid fishes of the genus *Salvelinus*. Dr. W. Junk Publishers, The Hague, The Netherlands. Pp. 631-666.

_____. 1980d. Comparative ontogeny of charrs. *In* E. K. Balon (ed.). Charrs: salmonid fishes of the genus *Salvelinus*. Dr. W. Junk Publishers, The Hague, The Netherlands. Pp. 703-720.

Blackett, R. F. 1968. Spawning behavior, fecundity and early life history of anadromous Dolly Varden, *Salvelinus malma* (Walbaum), in Southeastern Alaska. Res. Rep. No. 6, Alaska Dept. of Fish and Game. Juneau, AL. 85 pp.

Cavender, T. M. 1978. Taxonomy and distribution of the bull trout, *Salvelinus confluentus* (Suckler), from the American northwest. Calif. Fish Game 64:139-174.

Lagler, K., J. Bardach, R. Miller, and D. Passino. 1977. Ichthyology, 2nd ed. John Wiley and Sons, New York.

Leitritz, E., and R. C. Lewis. 1976. Trout and salmon culture. Calif. Dept. Fish Game, Fish Bull. 164. Sacramento, CA. 197 pp.

Robins, C. R., R. M. Bailey, C. E. Bond, J. R. Brooker, E. A. Lachner, R. N. Lea, and W. B. Scott. 1980. A list of common and scientific names of fishes from the United States and Canada, 4th ed., Amer. Fish. Soc. Spec. Publ. 12. Bethesda, MD. 174 pp.

Received 5 January 1987
Accepted for publication 12 June 1987

Honorary Life Members

Ewart M. Baldwin
Irven O. Buss
L. C. Cady
Charles D. Campbell
Robert L. Carr
Julian L. Culbertson
Rexford Daubenmire
Glenn Deitschman
R. A. Diettert
Bruce V. Ettling
William K. Ferrell
C. Clement French
Stanley P. Gessel
N. S. Golding
Phil Haddock
H. P. Hansen
Adolph Hecht
Kenneth Holmes
G. Brooks King
Rufus W. Kiser
Lewis and Clark High School Library (In memory of Thomas Large and J. G. McCracken)
Joseph W. Mills
Milton M. Mosher
Richard J. Naskali
Frank D. Nicol
Frances J. Schadegg
C. Gardner Shaw
Leona M. Sundquist
Oscar Sziklai
Robert F. Tarrant
Richard B. Walker
D. J. Wort

1987 Sustaining Institutional Members

Battelle Northwest, Richland, Washington
EG&G Idaho, Inc., Idaho Falls, Idaho
Potlatch Corporation, Lewiston, Idaho
The Washington Water Power Company, Spokane, Washington
Weyerhaeuser Company, Centralia, Washington

1987 Institutional Members

Boise State University, Boise, Idaho
British Columbia Institute of Technology, Burnaby, British Columbia, Canada
Central Oregon Community College, Bend, Oregon
Central Washington University, Ellensburg, Washington
Centralia College, Centralia, Washington
College of Idaho, Caldwell, Idaho
Eastern Montana College, Billings, Montana
Eastern Oregon State College, LaGrande, Oregon
Eastern Washington University, Cheney, Washington
Edmonds Community College, Lynnwood, Washington
The Evergreen State College, Olympia, Washington
George Fox College, Newberg, Oregon
Grays Harbor College, Aberdeen, Washington
Green River Community College, Auburn, Washington
Highline Community College, Midway, Washington
Idaho State University, Pocatello, Idaho
Lewis-Clark State College, Lewiston, Idaho
Lewis and Clark College, Portland, Oregon
Linfield College, McMinnville, Oregon
Montana College of Mineral Science and Technology, Butte, Montana
Mt. Hood Community College, Gresham, Oregon
North Idaho College, Coeur d'Alene, Idaho
Northern Montana College, Havre, Montana
Pacific Lutheran University, Tacoma, Washington
Pacific University, Forest Grove, Oregon
Peninsula College, Port Angeles, Washington
Portland State University, Portland, Oregon
St. Martin's College, Lacey, Washington
Shoreline Community College, Seattle, Washington
Simon Fraser University, Burnaby, British Columbia, Canada
Skagit Valley College, Mount Vernon, Washington
Southern Oregon State College, Ashland, Oregon
Southwestern Oregon Community College, Coos Bay, Oregon
Spokane Falls Community College, Spokane, Washington
University of Alaska, Fairbanks, Alaska
University of Idaho, Moscow, Idaho
University of Montana, Missoula, Montana
University of Puget Sound, Tacoma, Washington
University of Victoria, British Columbia, Canada
University of Washington, Seattle, Washington
Walla Walla College, College Place, Washington
Washington State Library, Olympia, Washington
Washington State University, Pullman, Washington
Western Washington University, Bellingham, Washington
Whitman College, Walla Walla, Washington
Whitworth College, Spokane, Washington
Yakima Valley College, Yakima, Washington

1987 Sustaining Individual Members

Donald J. Brown, Richland, Washington
Randall E. Brown, Pasco, Washington
Nelsa M. Buckingham, Port Angeles, Washington
George R. Fahnestock, Seattle, Washington
William H. Funk, Pullman, Washington
Gerald H. Haddock, Wheaton, Illinois
Donald Hanley, Seattle, Washington
Charles R. Hatch, Moscow, Idaho
Mary M. Hektner, Arcata, California
Francis R. Herman, Fairbanks, Alaska
J. Jerry Landye, Flagstaff, Arizona
Dennis E. Lavender, Vancouver, B.C.
John E. Mitchell, Fort Collins, Colorado
Howard R. Panik, Carson City, Nevada
William H. Rickard, Richland, Washington
Diane E. Robbins, Tacoma, Washington
Edward S. Schreiner, Port Angeles, Washington
Dale Stradling, Cheney, Washington
Robin J. Tausch, Reno, Nevada
Ronald J. Taylor, Bellingham, Washington
Daniel W. Uresk, Rapid City, South Dakota
Steven and Kathryn Hamilton Wang, Olympia, Washington
Shepard M. Zedaker, Christiansburg, Virginia

Northwest Science

General Information

Publication in *Northwest Science* is open to scientists in the basic, applied, and social sciences who are engaged in original or fundamental research. *Northwest Science* does not publish notes, letters, or bibliographic papers. All submissions are reviewed by at least two referees and one associate editor. While submissions from outside the Pacific Northwest are welcome, at least one author of all papers considered for publication must be a member of the Northwest Scientific Association.

Information for Authors—A complete copy of the *Northwest Science* "Information for Authors" is available from the Editor.

Page Charges—Page charges are currently $60 per printed page. Petition for partial payment or waiver of these charges should be directed to the Editor upon the manuscript's being accepted for publication.

Manuscripts—Submit three copies of the paper (including tables and figures) to the Editor. Manuscripts should be typewritten on 8½x11 paper and *double-spaced throughout (including abstract, acknowledgments, literature cited, tables, and legends for figures);* provide ample margins. Avoid unnecessary footnotes. Do not break words at the end of a line. Format and style of manuscripts should conform to general usage in recent issues.

An abstract, written in complete sentences and not exceeding 250 words, should precede every article. It should succinctly state the objectives, the experimental design, the principal observations, and conclusions of the paper. Authors are reminded of the diverse disciplines and readership served by the journal; with this in mind, the abstract should conclude with a sentence or two stating the broader significance of the paper.

Literature citations should have the author's name and year of publication in the text; e.g. (Jones 1978). Citations should be double-spaced and listed in alphabetical order at the end of the article.

Present all data in international (SI) units. English equivalents may be added parenthetically. Use the 24-hour clock (0600 and 2300) and continental dating (17 November 1982).

Equations should be presented camera-ready. Symbols should be large enough to be legible after a ⅓ to ½ reduction in size, but not overly large.

Tables should be typewritten (double-spaced) separately from the text. Original art work or glossy prints of photographs must be submitted for reproduction. Art work and lettering should be large enough (but not overly large) to provide clarity after a 50 percent reduction in size for printing. The author's name and figure number should be penciled on the back of each illustration. Provide a scale for distance on map illustrations. Legends for illustrations should be typed (double-spaced) as a section of the manuscript; do not use a separate page for each legend.

Length of manuscripts is limited to 15 pages of printed copy. Two typed pages are approximately equal to one journal page.

Authors of Biological Papers—On first mention, a species should be designated by common name followed by systematic binomial. For abbreviations and forms of titles for serial publications, follow the *BIOSIS List of Serials.* Consult with the *Council of Biology Editors (CBE) Style Manual,* 4th ed., for general information on manuscript preparation.

Correspondence—Correspondence will be between senior author and the Editor.

Editing—In addition to being reviewed by two referees and an associate editor, manuscripts will be edited for grammatical correctness and clarity.

Galley Proofs and Reprints—One set of proofs will be sent to the senior author for correction shortly before publication; proofs should be returned to the Editor within three days of receipt. Senior authors should inform the Editor of any change of address for handling proofs. Reprints must be ordered when the proofs are returned. A schedule of reprint prices will be sent to the author with the proofs.

Non-Profit Org.

BULK RATE
U.S. POSTAGE
PAID
PULLMAN, WA
Permit No. 1

Northwest Science

Quarterly Publication of the Northwest Scientific Association

---

Papers published in *Northwest Science* are indexed in *Current Contents, Science Citation Index, Biological Abstracts, The Zoological Record, Recent Literature Supplement to The Auk, Abstracts in Anthropology, Bibliography and Index of Geology, Chemical Abstracts, Bibliography of Agriculture, Forestry Abstracts,* and *University Microfilms.*

Northwest Science is offered in exchange to other colleges, universities, learned societies, and libraries. Publications sent in exchange should be addressed to Washington State University Library, Technical Services Division, Pullman, Washington 99164-5610, U.S.A.